

Making Evolution Visible, Controllable, and Useful:

A History of Early Experimental Evolution

A DISSERTATION

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## Acknowledgements and Personal Statement

Upon finishing and submitting my dissertation to the committee, I had a chance to reflect on everything that has happened in my life and in the world since I began graduate school in 2012. And by 2021, it feels as if events are developing and changing at a pace much faster than nine years ago. And along the way, I have carried this project and dissertation along with me, sometimes as a source of intellectual stimulation and development, and other times as an anchor weighing me down. Throughout the process, I reengaged the material with new ways of seeing and thinking about the world, ensuring that I remained embedded in the work itself.

I mainly studied biology during my undergraduate years, hoping to establish a career as an evolutionary biologist, a topic I had been enamored with since my freshman year in high school. I attended the University of Minnesota – Morris, a liberal arts campus of about 1,800 students, where I was encouraged to explore outside my field, and I began to take history classes on medieval and early modern Europe. I took enough classes to minor and then double major in history. Professor Jennifer Deane encouraged me to blend my interests in history and science, so I wrote essays on the biology behind Tulipmania and the inbreeding coefficient of the Spanish Habsburgs, for example. In biology, Professor PZ Myers introduced me to alternative views within evolutionary and developmental biology as well as providing the inspiration to engage in science blogging. Through this I became acquainted with Arlin Stoltzfus, a protistologist who was convinced that the history biologists told themselves about evolution was incorrect and even hid important scientific concepts, such as mutationism. I picked up on a concept that he focused on, the notion of creativity in evolution, and wrote about the history of creativity within evolutionary biology as my senior thesis. I also began to co-author a paper with Arlin arguing for a revision of the history of evolutionary biology, elevating “Mendelian-mutationism” as a “forgotten synthesis” prior to the orthodox development of the Modern Synthesis, which was published in 2014 in the *Journal of the History of Biology*. This blending of history and science, and acquaintance with alternative views of biology and history, were the key intellectual factors that I entered graduate school with.

During this time I also volunteered in the laboratory of Michael Travisano, where I became acquainted with experimental evolution. In this lab they had rapidly evolved unicellular yeast to become multicellular through a strict process of natural selection. Mike also introduced me to Mark Borrello, who became my adviser, and is how I discovered the University of Minnesota had a program in the history of science in the first place. Deciding that the laboratory life was not for me, I switched gears from biology to history of science, applied to the program, and I was accepted. Unsurprisingly, my dissertation project would be about the history of experimental evolution. I thank Mike for allowing me to become acquainted with the field as well as facilitating meetings with other practitioners at the Gordon Conference for Microbial Population Biology and the BEACON Center for the Study of Evolution in Action.

In my senior year my mother developed pancreatic cancer that took her life in about 1 year after diagnosis. She was 45. To her I credit a lifelong love of reading. As a kid she told me that she would never say no if I asked her to buy a book. About a month before she died, I was able to tell her that I had been accepted to graduate school to study the history of science at the University of Minnesota. I like to think that small bit of news helped her rest a little as she pondered what her children's futures would look like without her.

Graduate school itself, especially during the coursework years, was an enlightening, stimulating, and fun experience. I thank the other member of my cohort, Nicholas Lewis, for his laidback style of humor and camaraderie, as well as Maggie Berggren for her close friendship during these years. The graduate student office was I thank Cameron Lazaroff-Puck, Bonnie Gidzak, Jess Nickrand, Emily Beck, Liz Semler, Lauren Klaffke, Kate Jirik, Cosima Herter, Dustin Studelska, Will Vogel, Adam Fix, Emmie Miller, Macey Flood, Alexander Greff, John Heydinger, Anna Amramina, Sam Froiland, Felipe Eguiarte Souza for all of the wonderful interactions over the years.

Coursework and discussions with Mark, Susan Jones, Jennifer Alexander, Alan Love, and Michel Janssen showed me different ways to think about science and its history. In essence, I had joined the program as a somewhat naïve student who thought about science romantically, as about pure understanding of the world, which I think was somewhat due to my interest in evolutionary biology (as opposed to say, nuclear

physics). But through these interactions I began to see the other sides of science and examine it more critically. I soon saw experimental evolution as a way to *control* evolution. The nebulous concept of “control” became key to my project, a way to historicize and link experimental evolution to the world around which its practitioners worked (even if their laboratory work remained my focus). I thank Mark especially for encouraging and supporting this thematic development of the project, especially in the final months when I had the most trouble bringing the dissertation to a close yet needed to deepen my analysis.

My perspective had changed radically while dissertating in 2016. Obama’s second term was coming to an end with nearly zero progress on most issues. But activity in “the streets” – Occupy Wall Street, Black Lives Matter, and Standing Rock – dispelled the mirage of the end of history. At the same time, Senator Bernie Sanders waged a presidential campaign that cut through the prevailing narratives – against “Hope and Change,” against “Make America Great Again,” and against “America Is Already Great” – pointing to another way and popularizing socialism. However, Sanders lost, another Clinton won the nomination, who then lost to a grotesque and reactionary reality television host. This process increasingly produced a feeling of deep alienation as I wrote about early twentieth-century biologists experimenting with rats and maize. I was also rather isolated due to a summer followed by having a Doctoral Dissertation Fellowship, which meant I was not even TAing. This made Marx’s famous “eleventh thesis” hit especially hard: “the philosophers have only interpreted the world, in various ways; the point is to change it.”<sup>1</sup>

To relieve this anxiety, I joined a group called Socialist Alternative after I found myself on Interstate 94 during a post-Election Day protest they helped host. (I learned later the taking of the highway was a spontaneous action of the crowd and was not planned.) A funny thing about right-wing narratives about universities as radicalizing students was that my own turn towards Marxism took place *outside* the university education system. Through Socialist Alternative I learned more about Marx, Engels, dialectical materialism, Lewontin and Levins, and metabolic rifts, all while I helped the

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<sup>1</sup> Karl Marx, “Theses on Feuerbach,” Marxists Internet Archive, <https://www.marxists.org/archive/marx/works/1845/theses/theses.htm>.

Ginger Jentzen City Council campaign, the Kshama Sawant re-election campaigns in Seattle, 15 Now, and other practical activities. Intellectually what I discovered was not necessarily a new way of thinking, but rather a mode of thought that matched and bolstered my own. Thus, in the late stages of my dissertation, I once again reengaged with the material, tying the notion of control to capitalism. The prominence of the Marxist analysis varies throughout the dissertation admittedly, which itself reflects my own intellectual development: I did not begin with Marx, but for this dissertation to be *my* project as I finished it in 2021, Marx had to be in it. After submission I hope to develop the Marxist analysis of the dissertation's content further.

Because it is 2021, I do have to note that I finished the dissertation during the COVID-19 pandemic. For an ABD student, this did not play a major factor in the dissertation process, though it did slow me down: I was working an overnight unloading and stocking job at Target and the pandemic made an already physically taxing job even *more so*. As for the dissertation, what the pandemic entailed was an online defense over Zoom with no gathering of graduate students at a bar afterward. Instead, we marked my defense over Zoom, too.

Finally, present all throughout these events and developments, were my friends and family. My friends, Alex, Liz, Russ, and Max made my Friday nights every week, especially helpful during the stress of the coursework and preliminary exam years. My friend, Katie, was there for me through every twist and turn. I also thank the members of Socialist Alternative, our meetings and gatherings acted as an intellectual and social stimulus outside of academia. But most importantly, I thank my sister, Cassie, and her two children: my nephew, Ben, and my niece, Aubrey, to whom I dedicate this dissertation. Cassie, and her partner, Joey, regularly made the 80-100 minute drive to pick me up for weekend visits so that I could participate in Ben's and Aubrey's lives as they grow and learn.

While I hope to continue developing the project, doing so from outside academia will be a challenge, even if it amounts to 'only' a few papers. But now I finally part with the dissertation as a dissertation. As they say, a good dissertation is a done dissertation. And now it is done.

**Dedication**

To Benjamin Ross and Aubrey Ross

In memory of Jodi Cable

## **Abstract**

How to control evolution? This question has animated biologists for nearly 150 years and for breeders, some time longer. Charles Darwin's theorization of evolution by natural selection was in part an analysis of extant breeding practices, what he called an "experiment on a gigantic scale." Therefore, from its very beginning, the science of evolution was a study of how to control it, mediated by experimentation. This dissertation argues for the centrality of experimentation in the development of evolutionary biology. What is called experimental evolution today, a growing field of study popularized by Richard Lenski's Long-Term Evolution Experiment, is an elaboration upon a rich bedrock laid by long-neglected biologists and breeders. For this dissertation, I consider experimental evolution to be controlled studies of natural evolutionary processes, such as selection, mutation, and inbreeding, usually over multiple generations. Throughout the dissertation I examine the motivations of scientists, their epistemological arguments in favor of experimentation, the efforts they exerted to make it possible (such as building research institutions), their contributions to the science of evolution, as well as the influence of capitalism and how practice and theory interacted. Through their various methods, theories, and motivations, what emerged was the scientific desire to make evolution visible, controllable, and useful.



## Table of Contents

List of Figures .....	vii
Introduction .....	1
Chapter 1: “An Experiment on a Gigantic Scale” .....	29
Chapter 2: Making Evolution Visible .....	60
Chapter 3: A New Atlantis: The Station for Experimental Evolution .....	90
Chapter 4: Controlling Evolution?: Mutationism, Pure Line Work, and Genetic Selectionism .....	135
Chapter 5: “At Nature’s Mercy”: A Debate Over How to Control Evolution .....	188
Conclusion .....	249
Bibliography .....	268
Appendix I: Dallinger’s Machine and His Reception.....	280

## List of Figures

Figure 1: Reverend William Henry Dallinger’s microbial incubator .....	51
Figure 2: Raphael Weldon’s “experimental crabbery” .....	68
Figure 3: Feet from William Castle’s polydactylous guinea pigs .....	147
Figure 4: Examples from initial stock of Castle’s hooded rats .....	151
Figure 5: Pure lines of <i>Paramecium</i> isolated by Herbert Spencer Jennings .....	176
Figure 6: Selected hooded rats from Castle’s experiments .....	203
Figure 7: The Hagedoorns’ use of Vilmorin wheat as a natural experiment .....	207
Figure 8: A pure line of <i>Diffflugia</i> isolated by Jennings .....	220
Figure 9: Variation and heredity within a pure line of <i>Diffflugia</i> .....	221
Figure 10: Reverend William Henry Dallinger’s microbial incubator .....	269

## Introduction

How to control evolution?

This question has animated biologists for nearly 150 years and for breeders, sometime longer. Charles Darwin's theorization of evolution by natural selection was in part an analysis of extant breeding practices, what he called an "experiment on a gigantic scale." Therefore, from its very beginning, the science of evolution was a study of how to control it, mediated by experimentation. This dissertation argues for the centrality of experimentation in the development of evolutionary biology, traditionally sidelined in favor of field and theoretical studies. What is called *experimental evolution* today, a growing field of study popularized by press accounts of Richard Lenski's Long-Term Evolution Experiment, is not new, but an elaboration upon a rich bedrock laid by long-neglected biologists and breeders. For this dissertation, I consider *experimental evolution* to be controlled studies of natural evolutionary processes, such as selection, mutation, and inbreeding, usually over multiple generations. Throughout the dissertation I examine the motivations of scientists, their epistemological arguments in favor of experimentation, their contributions to the science of evolution as well as the influence of capitalism and how practice and theory interacted. Usually, the control of evolution was a primary focus. Through their various methods, theories, and motivations, what emerged was the scientific desire to make evolution *visible, controllable, and useful*.<sup>2</sup>

## Challenging the Darwin Industry

Although historians of science have sought to decenter the Great Men of History, Charles Darwin remains the organizing principle of the history of biology. For example, the eras of evolutionary studies can be delineated roughly as pre-Darwinian, the life of Darwin himself, the "Eclipse of Darwinism," and the Modern Synthesis, a.k.a., the restoration of Darwinism. Historians have written so much about Darwin that the term "Darwin Industry" was coined in the 1970s and has since become something of a

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<sup>2</sup> This formulation of the goals of experimental evolution came from a useful conversation I had with Susan Jones early in the project and helped me to orient the overall work.

pejorative.<sup>3</sup> I do not dispute that Darwin holds a central place in the history of biology, but that his centering often distorts our view of that history. Hence, the first chapter begins not with Darwin, but with the breeder Robert Bakewell.

With Darwin, the most important distortion from the perspective of this project is the perception of him as naturalist and theorist, rather than as experimentalist. The neglect of experimentation is evident in *The Cambridge Encyclopedia of Darwin and Evolutionary Thought* (2013): Of the sixty-three essays, none treat Darwin's experimental practice specifically, though several essays discuss experimentation in the twentieth century.<sup>4</sup> That in itself produces a double distortion: first, that Darwin's experimentation is not worth discussing in an encyclopedia containing his name and, second, that experimental evolution is a twentieth-century innovation, rather than originating in the nineteenth-century under Darwin's influence (and in some sense even preceding him). If experimentation is not central in an analysis of Darwin's theory, then experimental evolution's history is itself neglected.<sup>5</sup>

To characterize Darwin solely as a naturalist and theorist, however, is mistaken; the work of Janet Browne, Soraya de Chadarevian, and Richard Bellon, all demonstrate clearly that experimentation constituted much of Darwin's biological practice, especially after 1859.<sup>6</sup> While scholars usually emphasize the naturalistic and observational aspects

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<sup>3</sup> Lenoir, "Essay Review: The Darwin Industry," 115. Even though historians acknowledge the problems of continuing to focus so closely upon Darwin, he appears to have become no less important, considering the celebrations dedicated to the bicentennial of his birth and the sesquicentennial of *The Origin of Species* in 2009. Historians contributed their share: *The Cambridge Companion to the "Origin of Species"* in 2009 (while a *Companion to Darwin* had been published in 2003). In 2013, Michael Ruse published an edited collection of sixty-three essays entitled *The Cambridge Encyclopedia of Darwin and Evolutionary Thought*, dedicated to exploring the breadth of Darwin's work and his lasting influence across disciplines and geographies.

<sup>4</sup> Although "experiment" has a single entry in the index (to Joe Cain's essay on the Modern Synthesis), the topic actually comprises a substantial portion of Jean Gayon's essay on Darwinism in France post-1900 as well as Betty Smocovitis' essay on evolutionary botany from 1920 to 1950. David Rudge's essay on ecological genetics briefly mentions the experiments of Kettlewell on natural populations of moths. Strangely, Steven Hecht Orzack's essay, "The Evolution of the Testing of Evolution," contains no mention of experimental work on the topic, despite Gayon's essay in the same volume discussing that very subject. (In general, the *Encyclopedia* contains almost no cross-referencing.) The earlier *Cambridge Companions* similarly neglect experiment; in the latter, only Jim Endersby mentions any of Darwin's experimentation.

<sup>5</sup> In another compendium, Keller's and Lloyd's *Keywords in Evolutionary Biology* (1992), a mixture of history, philosophy, and science, philosophers and biologists are more likely to mix experimentation into their discussions than the historians, except for Diane Paul's essay on heterosis.

<sup>6</sup> Soraya de Chadarevian, "Laboratory-Science versus Country-House Experiments: The Controversy between Julius Sachs and Charles Darwin"; Browne, *The Power of Place*, 166–178, 182–183, 193, 201, 212, 241; Bellon, "Charles Darwin Solves the 'Riddle of the Flower'"; Bellon, "Inspiration in the Harness

of Darwin's practice – represented by biogeography, geology, and cirripedology, among other topics –, Browne and Bellon have made clear the importance of his experimental and material practices in convincing the scientific community that evolution was a workable scientific theory. His botanical studies were explicitly engaged to this end; both Asa Gray and Darwin considered *Orchids*, his first book after *The Origin*, to be a “flank movement upon the enemy.”<sup>7</sup> Bellon argues that Darwin, responding to the criticism that *The Origin* was too speculative and not properly inductive, turned to botany in order to “tie evolution to a productive mode of original investigation [, which] proved decisive for the scientific acceptance of evolution in the 1860s.”<sup>8</sup> Joseph Hooker told Darwin that he considered him “out of sight the best Physiological observer & experimenter that Botany ever saw.”<sup>9</sup> Darwin's continued botanical investigations testified to his commitment to experimental practice, including his last published words in a preface to Herman Müller's *Fertilisation of Flowers* (1883), in which he “exhorted the “young and ardent observer” to “observe for himself, giving full play to his imagination, but rigidly checking it by testing each notion experimentally.””<sup>10</sup>

Given the importance Darwin himself attributed to experimentation, why does it remain unappreciated? Why has it taken so long for historians to recognize this aspect of Darwin's life? While a complicated question, Bellon offers three suggestions: First, Darwinian floral botany waned by the end of the nineteenth century, particularly in the advent of new research traditions in genetics and Clementsian experimental ecology, and has been since forgotten.<sup>11</sup> Second, some of Darwin's experiments, particularly on plant movement, caused a debate with plant physiologist Julius von Sachs, of which de Chadarevian argues was actually about the rising barriers between laboratory and “country-house” experimentation. As biology professionalized, Darwin's style of amateur experimentation came to be regarded as illegitimate and thus not as respected by his scientific successors as they were by some of his contemporaries.<sup>12</sup> (But as I show in

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of Daily Labor”; Bellon, “Darwin's Evolutionary Botany.” Desmond and Moore do not stress Darwin's experimental side in their 1991 biography to the same degree as Browne.

<sup>7</sup> Bellon, “Inspiration in the Harness of Daily Labor,” 407–409.

<sup>8</sup> Bellon, “Charles Darwin Solves the ‘Riddle of the Flower,’” 383.

<sup>9</sup> Quoted by Ibid.

<sup>10</sup> Ibid., 387.

<sup>11</sup> Ibid., 395.

<sup>12</sup> De Chadarevian, “Laboratory-Science versus Country-House Experiments.” Neither de Chadarevian nor

Chapter 4, geneticist Edward East took his experiments on plant inbreeding seriously.) Third, historiographically speaking, historians have often ignored the daily practice of Victorian scientists.<sup>13</sup> Therefore, despite Darwin's centrality to the history of biology, much of his science remains unexplored, even decades following the "turn to practice."<sup>14</sup> The neglect of experimentation in evolutionary studies, then, is perhaps due more to the concerns and commitments of historians, rather than Darwin's own approach.<sup>15</sup>

A key difference between Darwin and his experimental descendants is that the latter gave experimentation an explicit ideological slant as the future of science. It is not evident that Darwin saw natural history as in conflict with experimentation, nor was he all that interested in controlling the evolutionary process itself. Darwin occupies an ambiguous role in the history of biological experimentation: he integrated experimentation with natural history in his own work and did so not only directly but also relied upon the work of breeders who exerted control over the process of evolution. He may not have shared Jacques Loeb's or Charles Davenport's ideology of control, but his method of treating breeding as a form of experiment was still controversial at the time (particularly with Alfred Russel Wallace). The first chapter of the dissertation centers this relationship between evolution and breeding both in history and in Darwin's own perspective on evolution.

### **The "Eclipse of Darwinism"**

Historians have long recognized that following Darwin's death, many turn-of-the-century biologists challenged aspects of his theory of natural selection (although rarely a

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Bellon discuss the details of Darwin's experiments, but instead focus upon the changing roles of experimentation within the scientific community as well as the social aspects of scientific community.

<sup>13</sup> Bellon, 396.

<sup>14</sup> See the recent work of Alistair Sponsel for how a focus on practice can transform our images of Darwin aboard the Beagle. Even Darwin's daily life on the Beagle has remained unexamined until recently! Sponsel, *Darwin's First Theory*. See also Hannah Landecker, "The Matter of Practice in the Historiography of the Experimental Life Sciences," in *Handbook of the Historiography of Biology*, eds. Michael Dietrich, Mark Borrello, and Oren Harman, (Cham: Springer, 2018): 1–22.

<sup>15</sup> Peter Bowler made a similar claim about evolutionary morphology: "Darwin himself had done important morphological work on the barnacles, but he did not participate directly in the creation of Haeckel's evolutionary morphology. In this case, the use of structural relationships to reconstruct the history of life on earth extended evolutionism into an area that Darwin himself did not regard as central. Precisely for this reason, the rise and fall of evolutionary morphology has gone largely unrecorded by historians. ... One is left with then with the impression that the whole episode should be regarded as something of an embarrassment." Bowler, *Life's Splendid Drama* (Chicago: University of Chicago Press, 1996), 13.

wholesale rejection). The “eclipse of Darwinism,” a phrase coined in 1942 by Julian Huxley, characterizes the period between Darwin’s death (1882) and the Modern Synthesis (1930s/1942) as a time in which “Darwinism” – or natural selection, specifically – fell out of favor with many biologists until it was reconciled with genetics.<sup>16</sup> While this period has often been viewed as scientifically stagnant and unproductive, a more careful interpretation is that a plethora of evolutionary theories flourished – including neo-Lamarckism, mutationism, Mendelism, and orthogenesis – that explored the possibilities of evolutionary mechanisms in the natural world, gardens, cropfields, and laboratories, and importantly, experimented with them.<sup>17</sup> Stoltzfus and I have argued that this period was essential for the future development of evolutionary biology; in this dissertation I further demonstrate that the experimental evolution of this period was also essential.

Until Peter Bowler’s *The Eclipse of Darwinism* (1983), historians had mostly ignored this period of evolutionary studies as they regarded it as not having produced anything scientifically noteworthy.<sup>18</sup> However, Bowler argued, if historians wished to understand the development of evolutionary thinking, they could not ignore the fifty years between Darwin (or Weismann) and Dobzhansky.<sup>19</sup> Even decades after Bowler’s

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<sup>16</sup> Provine, *The Origins of Theoretical Population Genetics*; Bowler, *The Eclipse of Darwinism*. It is important to note that Darwinism here refers only to natural selection. As Bowler showed in *The Non-Darwinian Revolution*, the biological community quickly accepted common descent, but not natural selection. Michael Ruse in *Monad to Man* has argued this quick adoption is because Darwin’s theory fit squarely into the Victorian ideology of progress. However, even an “eclipse of natural selection” should be qualified: so-called anti-Darwinists such as de Vries and Bateson accepted the existence of natural selection, but they did reject its creative power, which was one of Darwin’s major innovations Razeto-Barry and Frick, “Probabilistic Causation and the Explanatory Role of Natural Selection”; Stoltzfus and Cable, “Mendelism-Mutationism.”

<sup>17</sup> One step towards correcting the misconception that the Eclipse of Darwinism was a period of little scientific value might be to rid ourselves of the term “eclipse” altogether, as Mark Largent has argued. Largent, “The So-Called Eclipse of Darwinism,” 17–18. Much like the “Dark Ages,” Largent argues “eclipse” is a term “employed by the succeeding generation of authors to slur their predecessors by implying that they worked in an ignorant and ineffective era.” Ibid., 4.

<sup>18</sup> Bowler, *The Eclipse of Darwinism*, xvi. Even if this was the case, it is impossible to understand fully the history of biology, as well as the history of the social sciences and the intersection of science, politics, and culture without also understanding how evolutionary thinking, with its ties to notions of both cultural progress and deterioration, developed in the early twentieth century.

<sup>19</sup> Bowler had the additional purpose of responding to the creationist claim that Darwin has remained unquestioned by biologists; instead, he shows that there was a significant period in which natural selection was in fact challenged. In this vein, Jean Gayon has elaborated upon this analysis by showing that the natural selection of Darwinism is not the natural selection of today. Gayon, *Darwinism’s Struggle for Survival: Heredity and the Hypothesis of Selection*.

book, figures such as the Mendelians William Bateson, R. C. Punnett, and Thomas Hunt Morgan remain outside what is considered the history of mainstream evolutionary thinking, despite their essential contributions.<sup>20</sup> Historians still have a lot of work to do toward understanding this period; Sander Gliboff is currently reevaluating the history of neo-Lamarckism, for example.<sup>21</sup> What chapters 2-5 set out to do is understand some of the experimental side of this period.

The “eclipse of Darwinism” was when evolutionary studies were perhaps at their most experimental, or, at the very least, it was during this period that experimental evolution was first established. In fact, the biologist who first experimentalized evolution, at least from the view of his contemporaries, Dutch botanist Hugo de Vries, also constructed the mutation theory, frequently described as one of the major competitors to Darwinism (this despite de Vries’ feelings to the contrary).<sup>22</sup> In her paper, “The Battling Botanist,” historian Sharon Kingsland shows that Daniel MacDougal, director of the Carnegie Institution’s Desert Laboratory, championed the mutation theory precisely because it was experimentally-based (which also allowed for the control of evolution, more on which I discuss below).<sup>23</sup> Other significant figures who treated evolution experimentally – Frederic Clements, Paul Kammerer, C. E. Brown-Sequard – were neo-Lamarckians.<sup>24</sup> Overall, experimental evolutionists at this time had a complicated relationship with Darwinism, although several distinguished between Darwinism as theory and Darwinism as method (which I adopt). My analysis also further establishes the argument made by Stoltzfus and myself that while many of the Mendelians did not accept Darwin’s argument for selection’s creativity, they did not reject selection; rather, much of their work emphasized and approached the question of how selection works in a

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<sup>20</sup> Ibid.; Stoltzfus and Cable, “Mendelism-Mutationism.” In addition to contributing a new theory of heredity, the Mendelians reformulated Darwin’s natural selection to be “kinetic” (Gayon’s term) as it increased the proportion of one type over another, rather than gradually modifying the entire population over time. They also dropped the evolutionists’ commitment to gradualism.

<sup>21</sup> Gliboff, “The Case of Paul Kammerer.”

<sup>22</sup> Theunissen, “Closing the Door on Hugo de Vries’ Mendelism.” De Vries is also known as being one of the co-discoverers of Mendel, but Theunissen argues that this lens is the improper one for understanding de Vries on his own terms. That he ‘failed’ to integrate Mendelism into his scientific theory is to misunderstand de Vries.

<sup>23</sup> Kingsland, “The Battling Botanist.”

<sup>24</sup> Bowler, *The Eclipse of Darwinism*, 60–103; Bowler, *Evolution: The History of an Idea*, 234–245; Kohler, *Landscapes and Labscapes: Exploring the Lab-Field Border in Biology*.



Mendelian and mutating population.<sup>25</sup>

A key argument of my dissertation is that despite the complexity (and goofiness) of the period, the trend of experimental evolution led by the American geneticists, such as Edward Murray East and William Castle, was a serious endeavor. Paul Kammerer's fraudulent midwife toad experiment is perhaps the most well-known experiment of this era and its fame overshadows the careful experimentation of the Mendelians. Furthermore, while these scientists are frequently described as geneticists, I argue that experimental evolution may be a more fitting description for their work, including even Morgan and his students. I will argue in my subsequent chapters that, just as a focus upon Darwin can hide the experimental nature of biology during the nineteenth century, the common assessment of non-Darwinian theories as being unproductive misses the significance of the experimental nature of evolutionary studies during the period.

In our 2014 paper, my co-author Arlin Stoltzfus and I argued that Mendelian and mutationist biologists had been subject to historical revisionism that masked their major contributions to evolutionary biology. This was to make the Modern Synthesis appear more groundbreaking when it came to the relationship between natural selection and genetics. We called their work the “forgotten evolutionary synthesis.” We focused on the writings of five key and well-known biologists – Hugo de Vries, William Bateson, R. C. Punnett, Wilhelm Johannsen, and Thomas Hunt Morgan – and took their criticisms of Darwinism and their genetic and evolutionary contributions seriously. We discovered that many of their views were misinterpreted and sometimes outright misrepresented. For example, de Vries is almost always mentioned as having based his theory entirely on a single species, *Oenothera lamarckiana*, that ended up having an abnormal system of heredity, thus limiting the scope of his theory, or as is implied: De Vries was wrong.<sup>26</sup> However, his theory had a considerably broader evidential basis, including experiments

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<sup>25</sup> Ruse, *Monad to Man*; Gayon, *Darwinism's Struggle for Survival*.

<sup>26</sup> Kingsland's useful discussion of de Vries in “The Battling Botanist,” for example, emphasizes the primroses but does not give examples of his other sources of evidence. Some historians have challenged the usual dismissal of de Vries. Smocovitis, for example, claims that de Vries' work, “by drawing attention to the complex interplay of mechanisms at the chromosomal level, ... *Oenothera* drew attention to the power and utility of plants as tools for understanding patterns and modes of speciation.” Smocovitis, “Botany and the Evolutionary Synthesis, 1920-1950,” 315. Helen Anne Curry and Luis Campos, by tracing through botany the use of colchicine and radiation (respectively), have shown that de Vries had a lingering influence through work on polyploidy, the chromosomal aberrations de Vries is noted to have given undue influence on evolution.

with buttercups, and the persistent variation of *Draba verna*, as I elaborate in Chapter 2.

The relationship between our argument and this dissertation is important for the latter chapters. Our thesis was that Hugo de Vries made an essential critique of Darwinism by distinguishing for the first time between visible variation that was inheritable and visible variation that was not inheritable, labeled fluctuation and mutation, respectively. *Mutation was not defined as being large and significant variation, but instead as definite and inheritable (and eventually, random) variation.*<sup>27</sup> Such variation contrasted with fluctuations – variation that occurred due to environmental causes such as nutrition. (Thus, the common notion that one of the Morgan laboratory’s contributions was to demonstrate that mutations were frequently small was not a discovery or innovation, but a confirmation.) This distinction had major implications for how evolution worked, particularly how selection operated. This was a major disagreement with Darwin’s theory that gave rise to the notion that Mendelian-mutationism was a scientific dead-end. In our paper, we, building on the work of Jean Gayon, overturned this interpretation: the Mendelian-mutationists rejected Darwin’s notion that selection was creative, but accepted its importance. Their modifications to the theory of natural selection were ultimately transmitted to the Modern Synthesis, albeit with an orthodox Darwinian guise. The theory of selection that emerged from their experiments will be examined at length in Chapter 4 and 5.

While this dissertation does not focus upon elaborating upon our argument, it continues the overall argument. By focusing on a neglected set of biologists who pushed forward experimental evolution, such as William Castle and Edward Murray East, I discovered that they had taken up the “Mendelian-mutationist” arguments, for and against, in their own work. Indeed, the nature of selection was the major theoretical argument toward which they exerted their experimental efforts. Importantly, this debate was also over *how to control evolution* and clear concepts were fundamental to the task.

## Experimentation and the Control of Life

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<sup>27</sup> Stoltzfus and I separate de Vries from the others in that the latter hardened the distinction and contributed more positive

Historians of biology have emphasized that simultaneous to the “Eclipse of Darwinism,” the rest of biology underwent an experimental turn, the laboratory becoming a standard site of biological study. While a discipline such as embryology was long rooted in the laboratory, the microscope being its key instrument, it was not until scientists such as Wilhelm Roux and Hans Driesch began to intervene upon an organism’s natural development that the discipline became “experimental embryology.”<sup>28</sup> Following this shift, the history of late nineteenth- and early twentieth-century biology becomes a history of experimentalization across its subdisciplines, including morphology and ecology. But evolution is not usually viewed as one of the experimental subdisciplines of biology, the focus instead being upon genetics as a science of heredity and variation. What is required, therefore, is an attention to scientific practice and method: many American geneticists saw their work as being part of experimental evolution

The nature of the shift toward experimentation is a matter of debate among historians, centered upon what is called the “Allen thesis.” In 1978, historian Garland Allen claimed that early twentieth-century biologists “revolted from morphology” and became experimentalists.<sup>29</sup> Disappointed by the speculative nature of reconstructing evolutionary relationships via morphological and embryological differences, Allen argued that William Bateson and Thomas Hunt Morgan (among others) developed an experimental approach towards the problems of variation and heredity.<sup>30</sup> Responding to critiques, Allen reformulated his thesis the following year to state that the early twentieth-century biologists split into two camps: naturalists and experimentalists.<sup>31</sup>

In subsequent decades, several historians have challenged both formulations on

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<sup>28</sup> Maienschein, *Whose View of Life? Embryos, Cloning, and Stem Cells*, 67–68. Maienschein, responding to contemporary controversies such as President Bush’s halting of stem cell research development, shows how biologists have manipulated biological phenomena for centuries. For example, recombinant DNA research was controversial in the 1970s but has become rather mundane today. Overall, her book argues that the questions of “what is life” and “when does life begin” have changed frequently over time, but this is irrelevant to my purposes here.

<sup>29</sup> Allen, *Life Science in The Twentieth Century*.

<sup>30</sup> Peter J. Bowler has emphasized that Bateson’s and Morgan’s abandonment of evolutionary morphology did not kill this field of study. As with the events of the Eclipse of Darwinism generally, even if this work was *perceived* be a “sideline” to modern evolutionary biology, it does not mean this was the case. Bowler, *Life’s Splendid Drama*.

<sup>31</sup> Allen, “Naturalists and Experimentalists.” The key difference between the two forms is that Allen conceded the charge of category error: morphology is a biological discipline; experimentalism is a method.

grounds relevant to discipline and practice. For example, Jane Maienschein pointed out that the cytological work of E. B. Wilson – regarded as a triumph of laboratory biology – was more morphological and comparative than experimental; relatedly, Sharon Kingsland has noted that the Morgan lab’s program of chromosome mapping, too, was morphological, as it tended to ignore physiology and process.<sup>32</sup> Keith Benson argued that by dichotomizing biology, Allen distorted the methodological character of the various biological disciplines: for example, splitting embryology into descriptive and experimental work with a higher-level historiographical concept “obfuscates the understanding of the developments within each discipline.”<sup>33</sup> However, this assumes that the discipline is the proper historiographical category to analyze; thus, there is clearly a tension between the categories of discipline, identity, and practice.

Bowler made a similar point about evolutionary morphology. In addition to criticizing historians’ neglect of such work as well as the reconstruction of phylogenetic relationships because of Darwin’s lack of interest in such a project, he wrote: “The new historiography based on research traditions and professional disciplines tends to have the same effect as the old when it comes to evaluating the impact of evolutionism. ... The new historiography sidelines the impact of evolutionism because it did not form the basis of coherent professional groupings among biologists.” However, the “reconstruction of life’s ancestry was so extensive a project,” “a theme so broad that it could not be made the basis of a single research tradition,” that it “should be retained as a historiographical theme precisely because it served to connect a wide range of existing - and some newly emerging - disciplines.” I argue that the same applies to experimental evolution.<sup>34</sup>

This problem is particularly poignant when it comes to experimental evolution. Both historically and today, experimental evolution is not a discipline or a method, it is not unified by theory, and while it has coherent communities, it is not itself a community. Rather, it is an approach to evolutionary questions, which involves not only evolutionary biology as a discipline, but others that sometimes relate, such as agriculture,

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<sup>32</sup> Maienschein, “Shifting Assumptions in American Biology: Embryology, 1890-1910,” 94; Kingsland, “The Battling Botanist,” 205. I revise Kingsland’s perspective of genetics as morphology somewhat in Chapter 5: the Morgan lab integrated their mapping work into experiments on the operation of selection.

<sup>33</sup> Benson, “Problems of Individual Development,” 116.

<sup>34</sup> Bowler, *Life’s Splendid Drama*, 19-24.

microbiology, and molecular biology. This dissertation includes biometricians, proto-microbiologists, botanists, agriculturists and breeders, and geneticists, and a full account of experimental evolution would include microbiologists, molecular biologists, ecologists, and even chemical engineers. Thus, following experimental evolution is to take a tour through all of biology (although the degree it plays within any specific discipline varies considerably). What unites these figures I argue is *the control of evolution through experimentation*, to make it visible, controllable, and useful.

In science there is a double notion of control: to take power over the process or to limit the intervening variables that influence the process under study. Both are essential to experimental evolution: The object and goal of control change over time: sometimes they are restricted to theoretical questions, and at other times they seek the control of human evolution,

The notion that experimentation is the control of nature has its roots in the work of Sir Francis Bacon. As Carolyn Merchant argued in *The Death of Nature*, the Scientific Revolution was entangled with the rise of capitalism, the continued subjugation of women, and the exploitation of the environment. Merchant argued that philosophers such as Francis Bacon and René Descartes replaced an organic and holistic view of nature from the Renaissance with a mechanistic machine-like one. She claims that this mechanistic view of the world - ruled by prediction-making mathematical laws - “could legitimate the manipulation of nature” because “nature was now viewed as a system of dead, inert particles.”<sup>35</sup> According to Merchant, science is about power, control, and order. “In the mechanical world, order was redefined to mean the predictable behavior of each part within a rationally determined system of laws, while power derived from active

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<sup>35</sup> Merchant, *The Death of Nature: Women, Ecology, and the Scientific Revolution*, 193. At the same time, nature was associated with and likened to femininity, the apparent passiveness of which “legitimate[d] the exploitation and “rape” of nature for human good.” Ibid., 171. The tying of Francis Bacon’s philosophy of science to the subjugation of women has proven to be the most controversial claim of Merchant’s book. It is unfortunate that the focus of the debate does not appear to engage the other theses of the book, such as science’s ties to natural magic, commercial expansion, and environmental destruction as well as what role mechanistic thinking played in allowing the control of nature and of women. For the latest entry in the debate, which includes discussions of previous bouts, see Merchant, “Francis Bacon and the ‘Vexations of Art’: Experimentation as Intervention.”

and immediate intervention in a secularized world. Order and power together constituted control. Rational control over nature, society, and the self was achieved by redefining reality itself through the new machine metaphor.”<sup>36</sup> Merchant argues that this view of the world was most clearly represented in the work of Newton and Leibniz and thus imbues the world of physics. Due to experiment’s relatively late integration into biology in the late eighteenth century though physiology and embryology, Merchant did not address the topic.<sup>37</sup> But not coincidentally, Charles Davenport, who launched experimental evolution in the United States, pointed back to Bacon, even saying that with a Station for Experimental Evolution, Bacon’s “dream” could finally be made real. I discuss this at length in Chapter 3.

But Merchant’s thesis cannot be applied so straightforwardly to biology. The relationship between control and mechanistic thinking is more complicated. Darwin had a complex relationship with the notion of experimentation and control. He never put forward a vision of taking control of evolution, but did see it partially as already under control: the whole notion of selection, and change over time, and his theory of variation and heredity, largely came from the breeders who were actively working with evolution, an “experiment on a gigantic scale.” But regarding mechanistic thinking, Darwin is even more nuanced, yet informative: Donald Worster argued that Darwin had inherited the “well-oiled machine” of Linnean ecology and the mechanical utilitarianism of Paley’s natural theology, but that his theory “quietly laid an ax to the clock and broke it into smithereens. ... In a place of the world clock Darwin gave us the evolving tree of life. ... Darwin revealed a nature that is alive, messy, disorderly, unplanned, and seemingly chaotic.”<sup>38</sup> But Darwin did not throw the baby out with the bathwater: while he was not so mechanistic as some of his predecessors, his “entangled bank” was thoroughly *materialist*.<sup>39</sup> His theory therefore was based on control and implied control, even if his own writings did not center it and pointed to the complexities of doing so.

No biologist tied together the experimentalization of biology with the drive to

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<sup>36</sup> Merchant, *The Death of Nature*, 193.

<sup>37</sup> Coleman, *Biology in the Nineteenth Century*; Magner, *A History of the Life Sciences*.

<sup>38</sup> Worster, *Nature’s Economy*, 39; Worster, “Carolyn Merchant’s *The Death of Nature* at 25 Years,” 811.

<sup>39</sup> This is exactly what Karl Marx and Friedrich Engels saw as so valuable in Darwin’s work: that he, like they, had moved beyond “mechanical materialism” and made it dialectical: he had infused material nature with history, development, change, process, and interaction. I discuss this Chapter 2.

control as much as Jacques Loeb, emphasized by Philip Pauly's 1987 biography, *Controlling Life: Jacques Loeb and the Engineering Ideal in Biology*.<sup>40</sup> Pauly demonstrated how Loeb, working at the turn of the twentieth century, did not pursue his work for the sake of understanding the world, but for the sake of controlling it. For Loeb, experimentation was a way to manipulate living organisms to suit his desires. Justifying his approach through Ernst Mach, he disdained what he saw as the metaphysical speculations of evolutionists and morphologists. Mentored by the plant physiologist Julius Sachs, he sought to control the behavior of invertebrates such as tubularians, caterpillars, and sea urchins by adopting a physico-chemical and anti-vitalist view of biology, treating the organism as a machine manipulable by environmental stimulants such as light, gravity, and salts.<sup>41</sup>

Pauly summarized "the core of the Loebian standpoint" as "the belief that biology could be formulated, not as a natural science, but as an engineering science. More broadly, it meant that nature was fading away." Pauly continues,

As biologists' power over organisms increased, their experience with them as "natural" objects declined. And as the extent of possible manipulation and construction expanded, the original organization and normal processes of organisms no longer seemed scientifically privileged; nature was merely one state among an indefinite number of possibilities, and a state that could be scientifically boring. This transformation ... was a generalization from biologists' practice as they saw the extent of artificialization taking place in laboratories. Nature was disappearing, not as a result of argument, but through trivialization; not through disproof, but displacement. The natural became merely one among any results of the activity of biological invention.<sup>42</sup>

Thus, Pauly characterized the control or engineering of life as deemphasizing an understanding of the natural world as it is, rejecting the distinction between artificial and natural, and lacking interest in practical application.<sup>43</sup>

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<sup>40</sup> Philip Pauly, *Controlling Life: Jacques Loeb and the Engineering Ideal in Biology* (New York: Oxford University Press, 1987).

<sup>41</sup> For example, Loeb found he could cause a caterpillar to starve to death at the tip of the plant, even though food was nearby - in this instance, the "heliotropism" determined the insect's movement, not its need to nourish itself.

<sup>42</sup> *Ibid.*, 199.

<sup>43</sup> S. Andrew Inkpen's thesis is that biological/evolutionary thinkers have debated and renegotiated the relative worth of artificial and natural objects toward understanding how life works. For example, Wallace disagreed with Darwin's use of domesticated species (artificial) to understand evolution (natural); in a fascinating turn, in the 1940s, Dobzhansky, a major neo-Darwinian, agreed more with Wallace, abandoning

However, by focusing his work on Jacques Loeb, Pauly did not fully explore the picture of controlling life during the early twentieth century. For example, for much of his life, Loeb dismissed evolutionary studies as too full of metaphysical speculation and was thus not scientific. But by following Loeb, Pauly neglected contemporary events in experimental evolution: the dissertation's argument is that while Loeb may have been correct regarding late nineteenth-century evolutionary science, it was not entirely true of the early twentieth century. Furthermore, when placed alongside the scientists discussed in this dissertation, Loeb's position is rather extreme: for one, they combined experimentation and control with understanding nature, and they also sought utility rather than an aloof "engineering ideal." Even Pauly found Loeb's direct influence to be limited, not founding any kind of community like his contemporaries Morgan or William Keith Brooks.<sup>44</sup> While the experimental evolutionists showed less interest in how evolution worked in nature (or the wild) than non-experimental contemporaries, they occasionally worried over the question, an issue I discuss in chapters 4 and 5. (East, for example, wondered if methods of strict inbreeding matched any process in nature.) But as I will show in Chapter 3, especially, Charles Davenport, the head of the Station for Experimental Evolution, intended to integrate the natural with the artificial in a fruitful way, by searching for "laws" rather than the direct production of commodified stocks, although maize and poultry remained key species within experimental evolution to not only encourage funding but to be useful. Overall, experimental evolutionists did not emphasize such a distinction between artifice and nature and perhaps naively thought they need not worry about it, as opposed to Loeb who accepted the distinction but rejected orienting his research towards the natural.

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*Drosophila melanogaster* (which Kohler has considered to be a technological construction of the Morgan lab) for a more "natural" fly, *D. pseudoobscura*. Indeed, the artificial/natural distinction could be a reason experimental evolution is not always highly regarded by biologists, for many have a disregard for evolutionary hypotheses and results that originate inside a test tube. However, Kingsland argues that one of the key moves de Vries made with the mutation theory was to eliminate this distinction; indeed, she argues that de Vries, typically seen as an anti-Darwinian, strengthened Darwin's analogy between artificial and natural selection. Kohler, *Lords of the Fly: Drosophila Genetics and the Experimental Life*; Inkpen, "Denaturing Nature: Philosophical and Historical Reflections on the Artificial-Natural Distinction in the Life Sciences"; Kingsland, "The Battling Botanist," 492.

<sup>44</sup> Instead, Pauly traces strong intellectual influences on a few figures who became important in their own right: geneticist H. J. Muller, psychologists W. J. Crozier and B. F. Skinner, and the inventor of the oral contraceptive, Gregory Pincus. Pauly, 164–200. The diversity in disciplinary backgrounds of these figures indicates that a discipline-focused history might miss these connections.



Following Pauly, several historians also took up the theme of control, each showing how biology was experimentalized and controlled through various disciplines. Intriguingly, though, one has to dig for this theme as it was rarely the sole focus of a work: this includes Gregg Mittman's *The State of Nature* (1992), Lily Kay's *The Molecular Vision of Life* (1993), Adele Clarke's *Disciplining Reproduction* (1998), and Sharon Kingsland's *Evolution of American Ecology* (2005). Philosophers such as Ian Hacking also began to study the notion of "intervention" and not only "representations," as part of what he called a "back-to-Bacon" movement."<sup>45</sup> However, no synthetic work of controlling life has been written. Common themes have emerged, though, particularly the relationship between theory and practice, the role of patronage, and problems with the meaning of "control." This was part of a wider "turn to practice" within the history of science, although it did not fully embrace the history of evolutionary biology.<sup>46</sup>

Lily Kay adopted Hacking's distinction between representation and intervention to study molecular biology, but flipped the traditional picture of scientific development: molecular biology did not form as a discipline to create representations of life that would later produce applications; instead, "the goal of engineering life was inscribed into the molecular biology program from its inception."<sup>47</sup> A microscopic science such as molecular biology automatically entails control because intervention is required for understanding, such as X-ray crystallography and restriction enzymes. The same applies to some aspects of evolution, for experimentation (and statistics) was required to make it "visible," a major focus of Chapters 2, 4, and 5. This contrasts with a traditional picture in which historians and philosophers saw representations as preceding interventions (i.e., pure research leads to applications). But, when experimentation and patronage come into play, a one-way path from representation to intervention breaks down. For molecular

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<sup>45</sup> Philosopher of science Andrea Woody has made the critical point, however, that theory and models are a form of scientific practice also. Her example is the periodic table, which, while a representation, also actively categorizes the elements and upon its construction was only one way to do so. This point was emphasized by Nikolai Bukharin in 1931, whose perspective I discuss below. Woody, Andrea I. "Chemistry's Periodic Law: Rethinking Representation and Explanation after the Turn to Practice," in *Science After the Practice Turn in the Philosophy, History, and Social Studies of Science*, eds. Lena Soler, Sjoerd Zwart, Michael Lynch, and Vincent Israel-Jost (New York: Routledge, 2014): 123-150.

<sup>46</sup> See Hannah Landecker, "The Matter of Practice in the Historiography of the Experimental Life Sciences," in *Handbook of the Historiography of Biology*, eds. Michael Dietrich, Mark Borrello, and Oren Harman (Cham: Springer, 2018): 1-22.

<sup>47</sup> Kay, "Life as Technology: Representing, Intervening, and Molecularizing," 98.

biologists, to even *see* required *intervening* and that intervention is what organized their discipline.<sup>48</sup> My dissertation argues that this applies equally to evolutionary biology.

Intervention was not only for the sake of representation. “Just like Bacon’s program,” Kay argues, “the new biology should be understood on two nested levels of intervention”: the “proximate,” or the “technological control of life,” and the “ultimate,” or social control.<sup>49</sup> While scientists may have intervened solely for the purpose of understanding biology at the molecular level, the Rockefeller Foundation, Kay argues, invested in “psychobiology” in hopes of controlling society, whether through eugenics or psychiatry. Despite the disparate agendas, Kay shows that the proximate and ultimate interests “resonated” enough to facilitate scientific work.<sup>50</sup> As the head of the Rockefeller Foundation Max Mason said, the new science of molecular biology had “the aim of control through understanding.”<sup>51</sup> Intervention, representation, and control therefore intersect.

The scientific and sometimes political agendas of patrons has been established by historians as essential to understanding the development of the experimental biologies throughout the twentieth century.<sup>52</sup> For example, Kingsland has examined the relationship between patronage and control in ecology. The Carnegie Institution funded the MacDougal-directed Desert Laboratory to help develop experimental ecology, a discipline which Kingsland describes as a “broad eclectic subject [that] became a discipline because the science addressed larger American goals related to economic development. ... Ecology was connected to a larger quest for control over life that was

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<sup>48</sup> Ibid., 93. How different this is from other biological disciplines is debatable. One of the critiques of late nineteenth-century biology, for example, is that it was too focused upon the microscope. However, the microscope is not an instrument of intervention, but sense extension, whereas gel electrophoresis is a manipulation of molecules to create representations entirely different in kind. Maienschein differentiates descriptive and experimental embryology on the basis that the latter violates the “normal” by “contriv[ing] experimental conditions to create new access to normally hidden secrets.” Maienschein, *Whose View of Life? Embryos, Cloning, and Stem Cells*, 67.

<sup>49</sup> Kay, “Life as Technology: Representing, Intervening, and Molecularizing,” 91. See also Kay, *The Molecular Vision of Life: Caltech, The Rockefeller Foundation, and the Rise of the New Biology*, 18–19.

<sup>50</sup> Kay’s claim that molecular biology was funded in the United States for the purpose of social control is not well-supported and in fact engendered a heated exchange in the literature between Kay and a pair of molecular biologists. I discuss this below.

<sup>51</sup> Ibid., 46.

<sup>52</sup> Robert Kohler, *Partners in Science: Foundations and Natural Scientists, 1900-1945*, University of Chicago Press (1991).

shaping the direction of the life sciences in the early twentieth century.”<sup>53</sup> The interplay between the goals of scientist and patron are not always straightforward, but a clear alignment is found in Kingsland’s study of ecologist Frederic Clements, who engaged in experimental evolution, quantified the diversity of plant communities, and developed a theory of ecological succession modeled on the individual development of embryos, partially for the purpose of controlling nature. She writes,

The level of predictability also meant that the ecologist was potentially in a position to control the process. Ecological knowledge meant power over nature. It was not just a question of working in harmony with nature; that was a bit too passive. Once understood, the natural process could be retarded, accelerated, telescoped, held in one stage indefinitely, or deflected along another course, perhaps even destroyed in order to allow the process to start again. It could be manipulated and modified by inserting new species. It could be protected from all but climatic change.<sup>54</sup>

The ecology developed by Clements, Kingsland argues, was “a quintessential Progressive Era” science in that it focused on quantification, rationalization, prediction, and control.

Kay’s claim about the Rockefeller Foundation’s role in the origins of American molecular biology elicited a critical response from biologists Robert Sinsheimer and David Horowitz, who indignantly declared scientists’ independence from patron influence. Kay’s thesis was subtler than they portray: she emphasized that scientists themselves did not necessarily *desire* to develop their science to control society through molecular means, but that to obtain funding for their work (which, among other obstacles, required expensive instruments and a place outside traditional academic structures), they needed to orient their work to win Rockefeller funding. The degree to which scientists and patrons resonate changes on a case-by-case basis. Unfortunately, though, Kay left this part of the analysis underdeveloped: as Bentley Glass asked, did “social control” for

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<sup>53</sup> Kingsland, *The Evolution of American Ecology, 1890-2000*, 127.

<sup>54</sup> Kingsland continues: ““In short,” Clements argued, “as an instrument for the control of the entire range of human uses of vegetation and the land, succession is wholly unrivaled.” The value of the complex-organism lay in its power to confer on the human observer, the scientist, the ecologist, total control of a landscape to the extent permitted by the climate. Faith in the possibility of control stemmed from belief in the objectivity of science, the objectivity of quantitative, experimental methods, and the applicability of the organismic concept, which was for Clements no metaphor but a statement of objective fact. Solving problems of the kind presented by the Dust Bowl, which were foreshadowed in the degraded lands that Clements studied as a student, required the ability to predict exactly what would happen when humans entered a landscape and disturbed its natural progress.” Ibid., 151–152.

the Rockefeller mean “racial cleansing” or genetic therapy for diabetes?<sup>55</sup> Or perhaps such a distinction did not matter?

Adele Clarke’s study of the development of the “reproductive sciences” showed the importance of looking beyond the scientist-patron relationship for the implications of scientific control.<sup>56</sup> Because of the social implications and controversy surrounding the reproductive sciences, Clarke takes advantage of agendas and programs made explicit by her “social worlds”: eugenics, birth control, women’s rights, neo-Malthusians, philanthropies and foundations, and also the scientists themselves.<sup>57</sup> Unlike Kay’s work, the ways in which these social worlds seek to control life is quite clear.<sup>58</sup> Given the contrasting methods and agendas in the reproductive sciences, Clarke argues that the notion of “control” should be problematized, for it is “complex and multiple, unstable and difficult.”<sup>59</sup> First, “control,” frequently having negative connotations, can be used “for liberatory, repressive, unanticipated, and unknown other purposes.”<sup>60</sup> Even some of those who supported eugenics thought they were controlling heredity for the common good; for example, some women viewed eugenics as a path toward liberation from patriarchy.<sup>61</sup> Second, although “control” implies top-down force, the movement toward reproductive control was also advanced by grassroots movements, such as the birth control and women’s movements, showing that even lay women too sought to control life: their own reproduction.<sup>62</sup> Therefore, the social worlds “had varied goals, and power was far from equally distributed among them. But these are complicated stories of

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<sup>55</sup> Glass, “Review: Caltech and the Birth of Molecular Biology.” Kay does mention Pauling’s interest in “orthomolecular psychiatry,” but it is not developed. She also quotes Pauling making a quasi-eugenical statement about how people with sickle-cell anemia should wear stickers on their foreheads. How representative this is of Pauling’s views are left unclear. Kay, *The Molecular Vision of Life: Caltech, The Rockefeller Foundation, and the Rise of the New Biology*, 276.

<sup>56</sup> “Social worlds” theory, developed by Fujimira and Clarke, seeks to understand how the actions of individual actors coalesce into various “social worlds” that have a collective view of one problem of topic.

<sup>57</sup> It is worth noting that one of the inventors of the oral contraceptive is Gregory Pincus, one of the “Loebians” singled out by Pauly. Pauly, *Controlling Life*, 191–194.

<sup>58</sup> Lest it appear that I am overly critical of Kay, Clarke notes that when examining the archives of an institution like the Rockefeller Foundation, the “why” of social control is “almost invisible;” instead, one sees the “how” of where they spend their funds. Clarke, *Disciplining Reproduction*, 274. It is possible therefore that Kay could not precisely define what kind of control the Rockefeller officials were seeking.

<sup>59</sup> *Ibid.*, 24.

<sup>60</sup> *Ibid.*, 25.

<sup>61</sup> Susan Rensing, “Feminist Eugenics in America: From Free Love to Birth Control, 1880-1930,” PhD diss., University of Minnesota, 2006.

<sup>62</sup> Quoted by *Ibid.*, 26.

negotiations and trade-offs rather than simpler sagas of repression and denial.”<sup>63</sup>

Furthermore, “in the heterogeneous materialities of ordering and controlling life, there are no simple means of control - and certainly no innocent ones. Who gets to decide about the design and distribution of the means of control remains the central question.”<sup>64</sup> Thus, like Kay, and to some extent like Kingsland, the control of life for Clarke, was not merely the result of a hegemonic force dictating to scientists what should be done; instead, actors and groups, vying for their own interests, “resonated” through agendas of control, each negotiating and compromising their desires, whether such interventions were, in Kay’s terms, proximate or ultimate. Clarke’s examination of control is informative although it does not bear directly upon my dissertation as it has developed, not from disagreement but because it focuses exclusively on the interests of scientists. It is worth keeping in mind however that these scientists constitute one social world among others, such as the philanthropists, eugenicists, and agriculturists.

In Chapter 3, I examine the private and state patronage of experimental evolution, especially the Carnegie Institution’s founding of the Station for Experimental Evolution at Cold Spring Harbor. The addresses at its 1904 opening clearly show an interest among both scientists and the Carnegie for practical benefits from developing an experimental evolution. Because its director, Charles Davenport, also built and directed the Eugenics Record Office at the same site, and later merged with the Station, a similar question as Kay asked arises: what is the relationship between experimental evolution and eugenics?<sup>65</sup> It is not as straightforward as a 1:1 relationship: in fact, I show how eugenics did not appear in Davenport’s extensive application materials or in the opening addresses, but emerged over time and while eugenics came to dominate Davenport’s own work, it did not dominate the Station’s work as a whole. I address this further in Chapter 3 and in the conclusion.

Scientific developments do not automatically increase the ability to control and manipulate nature. For example, Kingsland notes that ecologist Henry Allan Gleason, who rejected the Clementsian paradigm of ordered succession, argued that plant

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<sup>63</sup> Ibid., 25.

<sup>64</sup> Ibid., 27.

<sup>65</sup> Kingsland, “The Battling Botanist”; Kohler, *Landscapes and Labscapes: Exploring the Lab-Field Border in Biology*.

communities were random assemblages, which “undercuts ecology’s usefulness.”<sup>66</sup> Bert Theunissen showed how Hugo de Vries’s mutationism, which rejected selection as a creative force, meant that both eugenics and mass selection as a method of crop improvement were for him non-starters.<sup>67</sup> (Unsurprisingly, biologists invested heavily in discovering ways to induce mutations so that they could gain control over evolution.<sup>68</sup>) That a theory could undermine scientific control shows that experimentation is not a straight path to controlling nature. Furthermore, competing theories are not just about best explaining the evidence, but also the degree to which control can follow from its postulates. Which evolutionary theory better facilitated control of the process itself was a main point of contention and worry among the experimental evolutionists in chapters 4 and 5.

Historians have thus highlighted how experimentalism co-evolved with the control of nature and that both relate to the surrounding social systems. What historians such as Carolyn Merchant, Lily Kay, and Sharon Kingsland have found regarding science and control, my dissertation argues also applies to experimental evolution in the early twentieth century. Merchant’s formulation of control as the combination of order and power is also useful. The biologists of this period took on the agenda of Francis Bacon, sometimes consciously, to both understand and control nature. As the biological sciences continued to expand, especially with the technological advances of biochemistry and molecular biology, the ability to control their subject has only increased. The extent to which experimentation and control define the subsequent history of evolutionary studies, however, remains an understudied topic, toward which my dissertation is a contribution.

### **The Historiography of Experimental Evolution**

Experimental evolution remains an understudied topic within the history of science. Typically, experiments are treated as the evidence for theoretical developments rather than as the primary motivation for the science, such as in William Provine’s *The*

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<sup>66</sup> Kingsland, *The Evolution of American Ecology, 1890-2000*, 160.

<sup>67</sup> Theunissen, “Knowledge Is Power.”

<sup>68</sup> Curry, “Accelerating Evolution, Engineering Life: American Agriculture and Technologies of Genetic Modification, 1925-1960”; Campos, *Radium and the Secret of Life*.

*Origins of Theoretical Population Genetics* and Peter Bowler's *Evolution: The History of an Idea*.<sup>69</sup> The result is that experimental evolution exists as a history in pieces and fragments in which it is rarely the primary subject itself. Thus, well-known figures in this dissertation, such as Hugo de Vries, Charles Davenport, and Alfred Sturtevant appear frequently in histories of biology, but usually not as the main protagonist and sometimes even as antagonists (if their theories or ideas opposed the mainstream). Others who feature prominently in this dissertation as main drivers of experimental evolution, such as George Shull and Edward East, are usually relegated to minor roles. In addition, I argue that a considerable amount of genetics, such as Wilhelm Johannsen's pure line theory and *Drosophila* work, should be reconstrued as experimental evolution, given the various ways in which they were taken up by contemporaries. So, my focus on experimental evolution as the subject brings a relatively novel set of actors to the fore and new motivations revealed.

Sharon Kingsland's 1991 article on "The Battling Botanist," Daniel MacDougal was among the first works to study experimental evolution for its own sake. As she wrote, studies of Hugo de Vries' mutation theory focused mostly on internal reception among scientists, thus requiring an analysis of how the theory was deployed by scientists to agitate for a broader program of experimentation and control. MacDougal made this motivation explicit when he said that power over mutations would overcome the gradualist commitment of evolutionary theory. Kingsland also viewed her study as an extension of Barbara Kimmelman's useful analysis of American genetics as emerging out of agricultural experiment stations, which I show is the same for experimental evolution more broadly.<sup>70</sup> Kingsland's article is an insightful study that established many of the central themes of the historiography of experimental evolution, which was unfortunately not taken up for a long period of time.<sup>71</sup>

In 2002, Robert Kohler's *Landscapes and Labscapes: Exploring the Lab-Field*

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<sup>69</sup> William B. Provine, *The Origins of Theoretical Population Genetics* (Chicago: The University of Chicago Press, 1971).

<sup>70</sup> Barbara Kimmelman, "A Progressive Era Discipline: Genetics at American Agricultural Colleges and Experiment Stations, 1900-1920," Ph.D. diss., University of Pennsylvania, 1987.

<sup>71</sup> Kingsland, "The Battling Botanist," *Isis* 82, no. 3 (1983): 163-204. In fact, Kingsland told me that she initially desired to write a book about the history of experimental evolution in the United States but abandoned it for what became *The Evolution of American Ecology*.

*Border in Biology* examined developments in experimental ecology and evolution, mostly in the field. His work is a counterpoint to the developments I examine which primarily occurred in laboratories and agricultural experiment stations. The scientists depicted by Kohler sought to pave a middle path between the “control and precision” of the laboratory with “the old naturalists’ breadth of vision and sympathy for living things.”<sup>72</sup> (In fact, these “border” biologists referred back to Darwin as a role model for their combined methods of natural history and experimentation.)<sup>73</sup> However, for the most part, Kohler argues that these biologists who lived in the “border zone” were not successful, one reason being that wild organisms are extraordinary difficult to control.<sup>74</sup> Partially the field naturalists were more interested in evolution in nature, rather than controlling it. The actors I examine, on the other hand, rooted themselves in laboratory and agricultural experimentation and for the most part sought organisms that were amenable to that experimentation. They still faced numerous challenges, but the pessimistic conclusions that come from Kohler’s history do not hold for this group.

Histories of experimental evolution did not appear for over a decade until Luis Campos’ *Radium and the Secret of Life*, in which a bulk of the work examines H. J. Muller.<sup>75</sup> Again, experimental evolution is not the focus, instead tracing the relationship between biology and radiation in the early twentieth century, but Muller’s and his contemporaries’ drive to induce mutations come to the fore. Muller happens to be one of the figures who Pauly pointed to as being influenced by Loeb and that shows through in Campos’ analysis: Muller wrote that he was after the “rainbow bridge to power,” but left unsaid what the power was for. In this way, Muller reflects the “engineering ideal,” moreso than his contemporaries that I examine in my dissertation. (Muller does appear in

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<sup>72</sup> Kohler, *Landscapes and Labscapes: Exploring the Lab-Field Border in Biology*, 26. That the biologists Kohler focuses on in his book, such as William Tower, Arthur Banta, among others, are unheard of today, speaks not only to the possible failure to produce substantial results, but perhaps also to the disregard of experimental evolutionists in general.

<sup>73</sup> *Ibid.*, 33.

<sup>74</sup> He also notes a number of other issues, such as lack of funding, institutional support, and workspace, as well as problematic organisms, faulty methods, and simply wrong ideas. Furthermore, Kohler highlights the problem brought upon by the advent of genetics for these border biologists: When Johannsen created the genotype/phenotype distinction, any evolutionary work conducted that had examined only phenotypes were now questionable. If a scientist did not distinguish between hereditary and non-hereditary traits, nothing conclusive regarding evolutionary phenomena could be derived from the study. According to Kohler, due to this combination of reasons, experimental evolution in the early twentieth century was a failure.

<sup>75</sup> Luis Campos, *Radium and the Secret of Life* (Chicago: University of Chicago Press, 2015).



Chapter 5 as a critic of William Castle.) Overall, Muller's career is a parallel to my dissertation, dedicated to inducing mutations, as opposed to the actors in Chapters 2, 4, and 5, who were interested more in studying the effects of selection and its relationship to mutation.

Helen Anne Curry's *Evolution Made to Order* is the historical work that has done the most to analyze twentieth-century experimental evolution but with a technological focus.<sup>76</sup> Curry focuses mostly on the mission to understand and induce mutations via radiation and colchicine. Chapter 3 of my dissertation covers the founding years of the Station for Experimental Evolution, but Curry takes up the institution in the 1920s and 1930s under the directorship of Charles Davenport's successor, Albert Blakeslee. Like Clarke's history of reproductive science, this is only a small part of her work, as Curry also examines other groups once mutation-inducing chemicals, particularly colchicine, became popular among casual gardeners. The degree to which the use of such chemicals became *useful* outside ornamental flowers was debatable, however, as shown by her discussion of General Electric's failed attempt to start a mutation-based plant-breeding program. Like Kohler and myself, she does not consider success or failure to be the arbiter of what is worthy of historical discussion.

Therefore, much work remains to be done on the history of experimental evolution and its control. My dissertation is a contribution to its development in the late nineteenth and early twentieth centuries. The dissertation is a combination of original research and work, especially on Dallinger, the Station for Experimental Evolution, and several parts of the debate I cover in Chapters 4 and 5, *and* significant interpretation of existing work, especially on Darwin and Mendel. Because there is little existing work on experimental evolution *as* experimental evolution, tracing its origins and boundaries within the considerable literature on the history of evolution is itself a crucial and important task. I begin with Darwin's and Mendel's relationship to experimentation, and early attempts at experimenting with evolution by William Dallinger, Raphael Weldon, and Hugo de Vries, as well as the establishment of the Station for Experimental Evolution at the turn of the century. I then examine the debate in the first decades of the

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<sup>76</sup> Helen Anne Curry, *Evolution Made to Order: Plant Breeding and Technological Innovation in Twentieth-Century America* (Chicago: University of Chicago Press, 2016).

twentieth century over the effects of selection on variation and heredity, centered primarily around William Castle, George Shull, Edward East, Herbert Spencer Jennings, and Raymond Pearl. I argue that the historiography of biology and evolution needs to integrate experimental evolution as one of the science's main currents alongside natural history, genetics, and theoretical population genetics. This should be done without regard to its successes and failures, but because scientists (and patrons) at the time centered it themselves as a crucial path to take to make evolution visible, controllable, and useful.

### **Dialectical and Historical Materialism**

Throughout the dissertation, I make use of dialectical materialism to better understand and conceptualize developments in the history of experimental evolution. I follow Marx, for example, in putting labor, materialism, and activity – experimentation, in this case – at the forefront of scientific change, rather than theoretical or idealistic developments. This inversion has become somewhat popular with the “turn to practice,” such as Kohler’s focus on *Drosophila* as part of material culture in *Lords of the Fly*. This also falls in line with the common understanding that thermodynamics and electromagnetism were theorized following intervention in the world. But the subtlety of the Marxist analysis of science – following particularly Nikolai Bukharin and Boris Hessen, captures several aspects of my dissertation’s argument quite readily.<sup>77</sup> First, by

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<sup>77</sup> In 1931 at the International Congress for the History of Science, a surprise delegation from the Soviet Union gave a series of lectures, published in English within a week as *Science at the Crossroads*. The delegation was led by the Old Bolshevik leader and theorist, Nikolai Bukharin, whose lecture interpreted the process of science through an Marxist approach that emphasized the integral role of labor and was targeted at idealism. Physicist Boris Hessen delivered another of the notable lectures, “The Social and Economic Roots of Newton's Principia,” emphasizing the material and social context of Isaac Newton; rather than treating him as a lone and isolated genius sprouting a revolution from his head, Hessen examined the capitalist and militaristic influences, such as the importance of understanding trajectories for ballistics. Zavadovsky gave a biological contribution combating idealism. Nikolai Vavilov, the internationally known botanist who infamously fell victim to Lysenko, was also part of this delegation, discussing his work on the geographical origins of agricultural varieties.<sup>77</sup> Nikolai Bukharin, “Theory and Practice from the Standpoint of Dialectical Materialism”; Boris Hessen, “The Social and Economic Roots of Newton's *Principia*”; and B. Zavadovsky, “The ‘Physical’ and ‘Biological’ in the Process of Organic Evolution,” from *Science at the Crossroads* (1931). Bukharin’s and Zavadovsky’s essays are indexed at <https://www.marxists.org/subject/science/index.htm>. They left a notable impact on British Marxist scientists, Haldane, Needham, Levy, and Bernal. Gary Werskey, *The Visible College: The Collective Biography of British Scientific Socialists of the 1930s* (New York: Holt, Rinehart, and Winston, 1979), John Bellamy Foster, *The Return of Nature: Socialism and Ecology* (New York: Monthly Review Press, 2020). Pietro Omodeo argues that the idealist (and to a large degree, internalist) trend within the history of

naming labor as the primary activity of humans, and around which society revolves, experimental evolution has a higher importance than just providing evidence for theoretical developments but is the primary way in which people (breeders, usually capitalists themselves) have engaged with evolution. Second, then, is that experimental evolution should be understood as developing from the society in which it formed, namely capitalism. Although my dissertation focuses on the technical work of biologists, I also point to and examine how their own capitalist context shaped their work (but did not fully determine it). In Chapter 1 especially I argue that Darwin and Mendel were theorizing what humans were doing in the (capitalist) world: taking control of evolution, a process which itself emerged from nature but became distinct from it. This relationship between capitalism and experimental evolution continues throughout the dissertation as it received funding from the Carnegie Institution, took place at U. S. agricultural experiment stations, and produced hybrid corn. Evolution was shaped by capitalism by more than just Malthus, but also at the intersection of experiment and control. Third, focusing on experimentation as primary does not relegate theory to a secondary position, for as Bukharin argued, theory itself is a special form of practice and the two remain distinct but interpenetrate. Marxism's capacity to see the relationship between theory and practice (and other traditionally opposed categories, such as natural and artificial) as one of unity and of difference is especially attractive in understanding the history of experimental evolution. Lastly, historians would typically engage with just historical materialism, but the history of science's unique positioning as studying a special relationship between humans and nature makes the *dialectical* aspects of Marxist thought more compelling.

### Structure of the Dissertation

Chapter 1, "An Experiment on a Gigantic Scale," reinterprets Darwin and Mendel in the history of experimental evolution. I open with Robert Bakewell, whose breeding practice

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science from Alexander Koyré to Thomas Kuhn was a reaction to the dialectical and historical materialism argued for by Bukharin, Hessen, and the British Marxists. Pietro D. Omodeo, "After Nikolai Bukharin: History of Science and Cultural Hegemony at the Threshold of the Cold War Era," *History of the Human Sciences* 29, no. 4-5 (2016): 13-34.

epitomized the control of evolution and made morphological and physiological changes visible to the world, especially Darwin. I also argue that Mendel's work, which is typically taught as the laws of heredity, is better seen as understanding and controlling evolution, or "artificial transformation." Therefore, the origins of evolutionary biology are rooted in experimental evolution, rather than experimental evolution being a later offshoot. I also examine the capitalist influences upon both figures, how they dealt with distinctions between artificial and natural, and how practice and labor preceded theory.

This chapter also discusses Reverend William Henry Dallinger, a figure entirely missed by historians of biology until now, although he is frequently mentioned by experimental evolutionists today. He conducted the first long-term selection experiment and used microbes, an experiment that began before Darwin's death. His remarkably early attempt and his understanding of it demonstrated many of the difficulties experimental evolutionists would face over the next century and a half: how to make the experiments actually work and produce results, and how to bridge the gap between evolution within a laboratory apparatus and evolution in the wild.

Chapter 2, "Making Evolution Visible," examines two of the first attempts to make experimental evolution itself a scientific practice. First, I examine Raphael Weldon, one of the chief Darwinian biometricians who famously feuded with William Bateson. I mostly avoid this debate which dominates the historiography. Instead, I follow the trajectory of his work with crabs from a purely statistical study to an astonishingly experimental undertaking. Although his work may not qualify strictly as experimental evolution for it was not a long-term multigenerational investigation of evolutionary mechanisms, I use it to examine the insufficiency of purely statistical methods to understand how evolution operated, signaling future developments. Second, I discuss Hugo de Vries, whose mutation theory dominated the science of evolution upon its publication. I show how de Vries had a broader evidential basis for his theory, including selection experiments and natural history, and discuss some of the key conceptual distinctions he made that proved essential to the trend of experimental evolution I follow in Chapter 4 and 5. Weldon and de Vries were transitional figures whose methods influenced much of the experimental evolution in the early twentieth century.

Chapter 3, “The New Atlantis,” examines the Station for Experimental Evolution in Cold Spring Harbor, New York. I briefly discuss early calls for such a dedicated institution among European biologists. Then I turn to Charles Davenport’s extensive and successful application to the Carnegie Institution of Washington to build and fund the Station. I show how broad Davenport’s vision of experimental evolution was (as opposed to being just genetics) and how both control and understanding nature were at the forefront. I also wade through its complicated and messy scientific work which followed many directions, sometimes fruitfully and sometimes as dead ends. And while it was also the home of the Eugenics Record Office, and eugenics soon dominated Davenport’s own work, I show that Davenport and the Carnegie did not build the Station with eugenical aims, thus making the connection between experimental evolution and eugenics not as straightforward as it would appear.

Chapters 4 and 5 are one continuous study of a notoriously extensive debate over pure line theory, the mutation theory, and the effectiveness of selection. I examine the technical development of the debate at length to better understand how experimentation impacted the theoretical developments that are usually the historical focus. This also helps illustrate the importance of controlling evolution during this period.

Chapter 4, “Controlling Evolution?: Mutationism, Pure Line Work, and Genetic Selectionism,” focuses on the work of the selectionist-geneticist William Castle and the pair of mutationist-pure linist botanists Edward East and George Shull. Castle’s experiments on small mammals convinced him that selection had the power to modify the hereditary material giving it evolution’s creative power. East and Shull, on the other hand, emphasized selection’s limits (but did not reject it) and instead relied upon hybridization, and inbreeding to overcome them. Thus two distinct theories of evolution and control emerged from their extensive experimentation. I also examine the work of Herbert Spencer Jennings, whose study of *Paramecium* corroborated East and Shull but with microbes (who were considered non-Mendelian). With the exception of Jennings, this work was funded by the Carnegie Institution and agricultural experiment stations.

Chapter 5, ““At the Mercy of Nature”: A Debate on How to Control Evolution,” continues this story as it erupted into debate, centered upon Castle’s hooded rats

experiments. East helped articulate multiple factor theory which incorporates continuous variation into Mendelism and undermined Castle's own interpretation of his work. Castle however relentlessly argued for his views and attacked his opponents. While East and Shull themselves did not participate in this debate, others rose to the task, especially Raymond Pearl and to a lesser extent H. J. Muller, the Dutch scientists the Hagedoorns, Castle's former student E. C. MacDowell, as well as Alfred Sturtevant and Calvin Bridges. Particularly crucial issues were methods and materials, the role of the environment, conceptual distinctions, and even an emergence of "population thinking." At its end, Castle conceded to his opponents while lamenting that evolution remained outside of human control and at "nature's mercy."

The Conclusion addresses lingering questions about experimental evolution's impact on the science of evolution, and points to the many directions future work on experimental evolution could fruitfully take now that my initial contribution is complete.

## Chapter 1: An Experiment on a Gigantic Scale

### Introduction

The attempts to control evolution long preceded the scientific understanding of evolution. Both Darwin's and Mendel's theories were rooted in what the former labeled "an experiment on a gigantic scale," the art and science of systematic breeding. Darwin in particular recognized that human societies had shaped evolution for thousands of years, and that breeders of plants and animals had just recently brought process and product under more direct willful control. That Darwin and Mendel emerged when and where they did — mid-nineteenth-century England and Moravia — is in retrospect no surprise given that both settings were centers of systematic selective and hybrid breeding. In this light, Darwin's and Mendel's theoretical contributions connected a systematizing practice that had emerged unconsciously, due to capitalist social relations, back to nature. While Darwin almost entirely relied upon the results of breeders, Mendel experimented with evolution directly. Therefore, what came to be known as "experimental evolution" was present in the very beginning of evolutionary science and formed much of the basis from which their theories of variation, inheritance, hybridization, and selection would spring.<sup>78</sup>

To that end, I first illustrate through Robert Bakewell how breeders began to take direct control of morphological and physiological evolution, which provided Darwin and Mendel the material evidence to formulate their theories of biological evolution and inheritance. That is, Darwin (and Mendel) provided theories to explain what the breeders had already accomplished in practice, although he had the broader aspiration of explaining all biological unity and diversity, natural and artificial. While the specific nature of pea plants has been emphasized as important for Mendel's work (as opposed to his later failure to work out the heredity of hawkweed), I also adopt Bert Theunissen's argument that Darwin's theory of selection was particularly shaped by pigeon fanciers, contributing further to the ties between theory and practice mediated by capitalism

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<sup>78</sup> This argument is reminiscent of one made by a Marxist named Paul Lafargue in "Economic Determinism and the Natural and Mathematical Sciences," *Social Democrat* 10, no. 3 (1906): 137, 145.

through amateur hobbies.<sup>79</sup>

I then discuss the first long-term selection experiment (of microbes) by parson-naturalist Reverend William Henry Dallinger. His work illustrates the enormous difficulties involved in experimental evolution, from setup, biological material, and equipment, to the active operation of the experiment itself, and the subsequent theoretical interpretations and extrapolations. I suggest that had Darwin taken up experimental evolution himself, it would be more reminiscent of Dallinger's work, than that of Weldon or de Vries, the subjects of the following chapter, largely due to the looser laboratory standards employed by amateur biologists prior to professionalization.

### **The Beginnings of Systematic Breeding in England**

The introduction of systematic selective breeding, or the control of livestock evolution, is surprisingly recent. While some varieties of dogs and livestock existed, Margaret Derry writes that “it is likely that most practices were haphazard in nature.”<sup>80</sup> Before enclosure, which planted the seeds of a capitalist economy in England, “mating was random and variation in type tended to relate to geographical districts.” Thus livestock and crops, tended to be adapted to local conditions, rather than adapted to meet specific standards, as a result of what Russell calls “domestic-environmental selection” (although at the time it could be explained by Lamarckian ideas). This was particularly the case for sheep who lived in semi-wild conditions unlike their draft animal brethren.<sup>81</sup> Indeed, the thoroughbred racing horse was the first breed of livestock created for a specific purpose — speed —, the result of repeated crossings of Arabian stallions with English mares.<sup>82</sup> The thoroughbred's emergence over the eighteenth and nineteenth centuries shows that *systematic selective* breeding, the oldest form of *evolutionary control*, is of recent invention.

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<sup>79</sup> Bert Theunissen, “Darwin and His Pigeons: The Analogy Between Artificial and Natural Selection Revisited,” *Journal of the History of Biology* 45, no. 2 (2012): 179-21; Peter J. van Dijk and T. H. Noel Ellis, “The Full Breadth of Mendel's Genetics,” *Genetics* 204 (2016): 1327-1336.

<sup>80</sup> Margaret Derry, *Masterminding Nature: The Breeding of Animals, 1750-2010* (Toronto: University of Toronto Press, 2014), 13.

<sup>81</sup> Nicholas Russell, *Like Engend'ring Like: Heredity and Animal Breeding in Early Modern England* (Cambridge: Cambridge University Press, 1986), 196–97.

<sup>82</sup> Bert Theunissen, “Darwin and His Pigeons. The Analogy Between Artificial and Natural Selection Revisited,” *Journal of the History of Biology* 45, no. 2 (2012): 201; Derry, *Masterminding Nature*, 14–17.



Few figures capture the ties between breeding, control, and evolution as well as Robert Bakewell (1725-1795), England's most prominent animal breeder in the late eighteenth century. Rather than relying upon crossing, the technique behind the thoroughbred, Bakewell developed his own breed of Leicestershire sheep through a combination of selection and inbreeding.<sup>83</sup> Contrary to the folk knowledge of the preceding centuries, Bakewell claimed that an animal's "blood" had a stronger influence over development than its environment. (This folk belief had begun to fade once farmers noticed that imported breeds could withstand the environmental change.) By selecting for improved traits of interest and "breeding in-and-in" the individuals who bore those traits, to a degree that astonished his contemporaries, Bakewell concentrated his improvements within the breed's "blood." In contrast to crossing, he developed a predictable method of controlling the evolution or genetic composition of his livestock. Although Bakewell's methods were only one of many, techniques being contingent on species, culture, purpose, and even personal preference, the point is that Bakewell introduced a systematic, formalized approach to the practice that produced visible morphological and physiological change over generations.<sup>84</sup>

One reason for the late arrival of systematic breeding was that to improve livestock in a given direction required ideological shifts. Historians Vítězslav Orel and Roger Wood claim that some breeders, including Bakewell, had come to think of domesticated animals as integrated machines — or "machines for turning herbage ... into money."<sup>85</sup> They were not automata, but dynamic and malleable. It had long been observed (since the ancient Greeks) that domesticates displayed more variability than their wild counterparts, a byproduct they attributed to changed environments. By 1700, breeders selected to *preserve* these characters.<sup>86</sup> However, the emerging belief that animals should be improved conflicted with natural theologians such as John Ray, who believed God's creations were already perfect; to him, selection should be used only to 'repair'

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<sup>83</sup> Derry, *Masterminding Nature: The Breeding of Animals, 1750-2010*, 17–18.

<sup>84</sup> Derry, 19.

<sup>85</sup> Quoted by Roger J. Wood and Vítězslav Orel, *Genetic Prehistory in Selective Breeding: A Prelude to Mendel* (Oxford: Oxford University Press, 2011), 38.

<sup>86</sup> Wood and Orel, 39, 48–49. As we will see, this observation regarding increased variability under domestication became a critical point of disagreement between Darwin and Wallace, the latter of whom rejected domesticates as a relevant example of natural selection.

degenerated breeds.<sup>87</sup> Others also considered inbreeding animals, as in humans, to be against God.<sup>88</sup> As late as 1810, agriculturist Richard Parkinson wrote to Joseph Banks, President of the Royal Society, that “changing things to extremes as some breeders have attempted, is setting themselves in opposition to their creator by endeavoring to destroy his works.”<sup>89</sup>

These conservative positions yielded in the wake of Bakewell’s ability to wield considerable power over the shape and physiology of his flock as well as by market desires for such. Sheep breeders had already selected for size and wool quality, as well as the removal of horns, but Bakewell focused on meat production: he bred for lighter and smaller bones, larger rib cages, and smaller heads and necks, so as to maximize the amount of meat as well as the speed at which sheep fattened. The short legs he developed prevented lambs from being able to nurse, a mistake that Bakewell then reversed (whether by selection or crossing is unknown).<sup>90</sup> Bakewell’s power to control evolution, whether real or alleged, was unprecedented.<sup>91</sup>

Bakewell’s need for profits combined with his theory of breeding produced a method that foreshadowed later experimental standards. Rejecting emphases on “purity” and ancestral heredity, he practiced a method akin to the present/future-oriented “progeny test.” Although he held that the “blood” was independent from the environment, he introduced a method of standardization for the dual purposes of establishing an experimental controls while optimizing a breed’s potential (e.g., wool quality partially depends upon climate and nourishment). Bakewell raised individuals of different breeds born at the same time on the exact same food regimen, eliminating environmental variation. To carry this out, he engineered his 450-acre farm, equipped with a mill and a canal, to efficiently transport materials, provide stable housing, and produce all the animal feed required. Upon their maturity, Bakewell experimented with his rams, leasing

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<sup>87</sup> Wood and Orel, 39. According to the authors, this “plastick Nature” meant that God did not have to micromanage the variations that resulted from an artificial environment.

<sup>88</sup> Wood and Orel, 195–96.

<sup>89</sup> Quoted by Wood and Orel, 79.

<sup>90</sup> Wood and Orel, 75–79.

<sup>91</sup> There is uncertainty over how much Bakewell’s methods were actually successful. Russell points out, for instance, that Bakewell sought for improved food conversion efficiency among his sheep, but the necessary weighing instrumentation did not exist, so Bakewell selecting on this basis is unlikely. Russell, *Like Engend’ring Like: Heredity and Animal Breeding in Early Modern England*.

them out to other farmers and assessing the quality of their offspring under changed conditions in different pairings. This also allowed him to check against the negative effects of his extreme inbreeding.<sup>92</sup> Thus the proper judge of an individual's breeding quality was not in its ancestral records, but in its demonstrable offspring based upon careful environmental control. These would become the basic tools of the geneticists over one hundred years later.

Bakewell also helps demonstrate that from the very beginning, "experimental evolution" or processes akin to it, is tied to political economy. Foreshadowing the dominance of the twentieth-century seed companies, this form of systematic selective breeding was feasible only for men who owned land.<sup>93</sup> Russell points out that small farmers had their own system of breeding, at least with cattle, in which they leased "common bulls" held by the parish. This social relation produced its own "breeding structure," in which "more cows were inseminated by one bull than was likely to have been the case with the herds of private owners of bulls. The potential for selective breeding was therefore greater, although the realisation of any scheme of improvement would seem unlikely," particularly because the bull itself was likely of low quality.<sup>94</sup> Thus from different social relations emerged various breeding practices even within the same counties.

Furthermore, Bakewell's intentions for his sheep reoriented the species along new capitalist lines. Because sheep needed to survive on their own for long periods of time, and consequently bred freely, they remained a "semi-wild" animal in which natural selection played a dominant role, as shown by the geographic differences among varieties dependent upon their specific environments. Before Bakewell, sheep were not bred to have specialized traits, due to being a multi-purpose animal that supplied meat, milk, wool, usually low quality, and helped fertilize fallow land. However, Russell describes Bakewell's "*economic objective*" as "the creation of a profitable meat animal," particularly through faster growth rates, efficient food conversion of fodder into meat, and reshaping its form to maximize the profitable cuts on its body. The focus on efficient

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<sup>92</sup> Wood and Orel, *Genetic Prehistory in Selective Breeding: A Prelude to Mendel*, 59–65, 82–84, 93.

<sup>93</sup> Russell, *Like Engend'ring Like: Heredity and Animal Breeding in Early Modern England*, 197.

<sup>94</sup> Russell, 150.

food conversion entailed changes to the sheep's lives: minimizing walking and other forms of activity, for example.<sup>95</sup> The notion of a "profitable meat animal" additionally necessitates the existence or creation of a market for such meat, which had not emerged until post-medieval times. Therefore, Bakewell transformed the dominant pressure upon his sheep from domestic-environmental and natural selection to artificial selection.<sup>96</sup>

Bakewell demonstrated the power of breeding. Humans were capable of more than simply perpetuating a variety or preventing its deterioration but could actively create new forms according to economic demands. Due to his interest in keeping the source of his profits secret, his influence was not so much in the specific technique and theories he developed, but instead was the power he visibly wielded. (There were also the difficulties of putting his ideas into practice and the contradictory obsession among many breeders for purity.)<sup>97</sup> Bakewell's construction of a farm dedicated to the modifications of organisms, and his visible and economic success, signaled future possibilities. The growth of systematic breeding throughout the nineteenth century then allowed Darwin to argue that evolution through practice had already been made visible, controllable, and useful. For as German agronomist Albrecht Thaer asked,

Did not Bakewell reduce the skeleton of his sheep by up to one half in weight while at the same time doubling the weight of flesh? Did he not change the shape of these animals in any way he wished?<sup>98</sup>

### **Charles Darwin, Breeding Theorist**

The work of the systematic breeders set the stage for the scientific achievements of Charles Darwin and Gregor Mendel; indeed, they can be thought of not only as fathers of evolutionary and genetic science, but as a unique pair of breeding theorists. I argue that Darwin was himself an experimental evolutionist, indirectly, by exploiting the social divisions of labor in British society. Although he never conducted a proper selection

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<sup>95</sup> Russell, 199–200.

<sup>96</sup> I can only suggest here, and take up somewhat in the conclusion, that this shift had significant environmental consequences and is an example of Marx's metabolic rift. Foster, John Bellamy, *Marx's Ecology: Materialism and Nature* (New York: Monthly Review Press, 2000).

<sup>97</sup> Russell, 219–220; Wood and Orel, *Genetic Prehistory in Selective Breeding*, 92.

<sup>98</sup> Quoted by Wood and Orel, *Genetic Prehistory in Selective Breeding: A Prelude to Mendel*, 119.

experiment, he paid attention to contemporary developments that pointed in that direction, such as Dallinger's work, but more crucially used artificial selection and domestication as experimental interventions of a sort. He did however conduct long-term inbreeding experiments with plants, which I discuss briefly in Chapter 4 when Edward East challenged his conclusions.<sup>99</sup> But what makes Darwin not just a mere "breeding theorist" is that his goal for evolutionary science was not to control nature, but to understand and explain it.

Although Darwin is frequently portrayed as a naturalist and theorist, due to his extensive work in biogeography, geology, and the natural history of barnacles, he was equally an experimentalist. For example, Richard Bellon has shown that Darwin's first post-*Origin* work, the *Fertilisation of Orchids* (1862), was a "flank movement upon the enemy" in that it "tie[d] evolution to a productive mode of original investigation, prov[ing] decisive for the scientific acceptance of evolution in the 1860s."<sup>100</sup> That is, not only did he engage with experimentation, he considered it to be of decisive importance in evolutionary science. In fact, in his last published words, in a preface to Herman Müller's *Fertilisation of Flowers* (1883), Darwin "exhorted the 'young and ardent observer' to 'observe for himself, giving full play to his imagination, but rigidly checking it by testing each notion experimentally.'"<sup>101</sup>

However, Darwin's commitment and apparent love for experimentation did not include direct experimental evolution. He famously tested dispersal patterns of seeds in marine environments, for example, but he did not experimentally practice selection over generations to test its effects. Because he never explained why he did not pursue such studies, we can only speculate. One factor certainly includes his theoretical commitment to gradualism, which would prevent seeing such an experiment as feasible or valuable – in fact, much of later experimental evolution centered upon grappling with gradualism, making evolution visible. The extraordinary difficulties likely also played a role as we will see in the work of his contemporary, Reverend Dallinger, which when combined

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<sup>99</sup> Charles Darwin, *The Effects of Cross and Self Fertilisation in the Vegetable Kingdom* (1876).

<sup>100</sup> Richard Bellon, "Inspiration in the Harness of Daily Labor: Darwin, Botany, and the Triumph of Evolution, 1859-1868," *Isis* 102, no. 3 (2011): 383.

<sup>101</sup> Richard Bellon, "Charles Darwin Solves the 'Riddle of the Flower,' or, Why Don't Historians of Biology Know About the Birds and the Bees?," *History of Science* 47 (2009): 387.

with his chronic illnesses, would have added even more stress. But perhaps a more productive question to pursue is: how did Darwin view the relationship between experimentation and the mechanisms of evolution?

Darwin's 1859 and 1868 publications, *On the Origin of Species* and *The Variation of Animals and Plants Under Domestication*, studied evolution under human command to explore the workings of nature, a controversial position.<sup>102</sup> Darwin's collapsing of a distinction between nature and artifice can be seen when he argued,

No doubt man selects varying individuals, sows their seeds, and again selects their varying offspring. But the initial variation on which man works, and without which he can do nothing, is caused by slight changes in the conditions of life, which must often have occurred under nature. Man, therefore, may be said to have been trying *an experiment on a gigantic scale*; and it is an experiment which nature during the long lapse of time has incessantly tried.<sup>103</sup>

Philosopher Andrew Inkpen has discussed how Darwin's contemporaries, particularly Alfred Russell Wallace and Charles Lyell, were skeptical of this use of breeding. They thought that domesticates, which varied more than their wild relatives and appeared temporally unstable, were too artificial to apply to nature.<sup>104</sup> But as this quotation shows, Darwin did not accept such a rigid distinction: both "Man" and "nature" have experimented upon the same initial variation caused by "slight changes in the conditions of life." As we will see, he did not think of them as totally identical, but not as entirely different, either; instead, he treated them dialectically, exploring one as informative of the other.

Eduardo Wilner substantiates Darwin's "Man" as "a legion of sloppy laboratory technicians," the breeders, who worked outside a coordinated scientific framework.<sup>105</sup> In Darwin's eyes, this work amounted to a kind of exploratory and natural experimentation.

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<sup>102</sup> I note here that much of Darwin's own experimentation as well as his reading of breeders was not related to selection, specifically, but the processes of variation and heredity.

<sup>103</sup> Charles Darwin, *The Variation of Animals and Plants under Domestication*, vol. 1 (London: John Murray, 1868): 3.

<sup>104</sup> S. Andrew Inkpen, "Denaturing Nature: Philosophical and Historical Reflections on the Artificial-Natural Distinction in the Life Sciences" (University of British Columbia, 2014).

<sup>105</sup> Eduardo Wilner, "Darwin's Artificial Selection as an Experiment," *Studies in History and Philosophy of Science Part C: Studies in History and Philosophy of Biological and Biomedical Sciences* 37, no. 1 (2006): 26-40.

While this framing is enlightening, it should not be taken too literally. Breeders such as Bakewell belonged more to Darwin's class and were not "technicians," in that scientific knowledge was incidental to the primary goal of financial profit, or in the case of pigeons, aesthetic pleasure.

Indeed, Darwin thought that breeding was evolution made visible, controllable, and useful, despite his own apparent lack of interest in the latter two. For Darwin, breeding's primary utility was not financial profit, but as evidence of a similar process in nature and specifically of natural selection. Even here though, the distinctions were not absolute, for he asked, "is it an illusion that these recently improved animals [the Hereford cattle breed] safely transmit their excellent qualities even when crossed with other breeds? ... Hard cash, paid over and over again, is an excellent test of inherited superiority." Thus, within the world of artifice, profit (a proxy for survival) was the standard by which an individual was judged and propagated. This rhetoric was essential for Darwin's theory.<sup>106</sup>

That Darwin thought artificial selection was so informative of natural selection was not a result of treating the former as a metaphor for the latter; rather, rhetorician Oren Abeles suggests that Darwin's comparison is actually a *metonym*.<sup>107</sup> Metaphor compares objects across categories whereas metonymy reduces a complex object into a simple one. Darwin's controversial move was to consider artificial selection a *type* of natural selection, reduced to its most visible and understandable form. The modern art of breeding unraveled the "entangled bank" of causes and effects, allowing Darwin to establish natural selection as a *vera causa*. It is in this way that breeding functioned as an experiment: breeders unconsciously imported natural objects into quasi-artificial environments and enacted a natural process through a (apparent) monocausal and tractable form.

Abeles further argues that what allowed Darwin to slide between artificial and natural selection, two seemingly exclusive categories, was the rhetoric of "incrementum."<sup>108</sup> In *The Origin*, Darwin co-opted a contemporary and self-congratulatory narrative that

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<sup>106</sup> Margaret Derry notes that Darwin's perspective was misguided: many cultural and social factors influenced a particular stock's price as well, especially when it came to notions of purity. Derry, *Masterminding Nature*, 33.

<sup>107</sup> Oren Abeles, "The Agricultural Figures of Darwin's Evolutionary Rhetoric," *Quarterly Journal of Speech* 102, no. 1 (2016): 41–61.

<sup>108</sup> Abeles, 46, 48.

nineteenth-century breeders were the cultural culmination of a millennia-long trajectory of domestication. Accepting, but slightly challenging this Whiggish narrative, Darwin wrote,

It may be objected that the principle of selection has been reduced to methodical practice for scarcely more than three-quarters of a century... But it is very far from true that the principle is a modern discovery.<sup>109</sup>

Darwin distinguished the “methodical selection” of nineteenth-century English breeders with the practices of the “barbarous periods of English history” (as well as those of the ancient Chinese and Romans), and, reflecting the developmentalist narrative, among contemporary “savages in South Africa.” To him, ancients and “savages” practiced

a kind of Selection, which may be called Unconscious. ... I cannot doubt that this process, continued during centuries, would improve and modify any breed, in the same way as Bakewell ... [who,] by this very same process, only carried on more methodically, did greatly modify, even during their own lifetimes, the forms and qualities of their cattle. Slow and insensible changes of this kind could never be recognised unless actual measurements or careful drawings of the breeds in question had been made long ago, which might serve for comparison.<sup>110</sup>

Darwin also used breeding as a natural experiment to demonstrate that unconscious selection can occur even under methodical selective regimes. William Youatt, a veterinary surgeon, reported that two breeders had each kept their own herds of Bakewell’s “purely bred” Leicester sheep, and “yet the difference between the sheep possessed by these two gentlemen is so great that they have the appearance of being quite different varieties.”<sup>111</sup> (This is reminiscent of Darwin’s analysis of South American rheas.) Darwin extrapolated the results of this experiment to claim that selection is a natural tendency of humans: “in a vast number of cases we cannot recognise, and therefore do not know, the wild parent-stocks of the plants which have been longest cultivated in our flower and kitchen

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<sup>109</sup> Charles Darwin, *The Origin of Species by Means of Natural Selection: Or, the Preservation of Favored Races in the Struggle for Life* (1859): 33.

<sup>110</sup> Darwin, 34–35. Darwin’s argument is the dialectical notion of quantitative changes producing a qualitative transformation.

<sup>111</sup> Darwin, 36. Abeles shows that Youatt, which Darwin read enthusiastically, was who offered Darwin the metonymy he later used. Abeles, “The Agricultural Figures of Darwin’s Evolutionary Rhetoric,” 55.



gardens.”<sup>112</sup>

Darwin’s introduction of “natural selection” to the narrative was in this gray zone of “incrementum” between nature and artifice:

In regard to the domestic animals kept by uncivilised man, it should not be overlooked that they almost always have to struggle for their own food, at least during certain seasons. And in two countries very differently circumstanced, individuals of the same species, having slightly different constitutions or structure, would often succeed better in the one country than in the other, and thus by a process of “*natural selection*,” ... two sub-breeds might be formed. This, perhaps, partly explains ... [why] the varieties kept by savages have more of the character of species than the varieties kept in civilised countries.<sup>113</sup>

Thus, not only did Darwin treat artificial selection as a type of natural selection, he introduced his controversial term in the context of domesticated livestock living in natural conditions (such as British sheep before Bakewell). Darwin’s use of incremental and metonymic rhetoric provided him a way to blur the lines between them while keeping them distinct. The qualitative distinctions between natural and artificial selection arose from differences in complexity (such as competing selective forces) and time, but at root they shared an identity.<sup>114</sup> Abeles concludes,

The *Origin* is grounded in that climactic narrative, with Darwin’s combination of tropes articulating an incremental alignment of nature and culture, in which the breeder’s metonymic power stands as a summation of the selective efficacies that culturally precede it.<sup>115</sup>

Ironically, despite Darwin’s emphasis on breeders wielding his *vera causa*, Darwin presented a limited picture of breeding practices. Historian of breeding Bert Theunissen argues that in *The Origin* and throughout his life, Darwin downplayed the importance of

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<sup>112</sup> Darwin, “The Origin of Species by Means of Natural Selection,” 37.

<sup>113</sup> Darwin, 38. Emphasis mine.

<sup>114</sup> Abeles, “The Agricultural Figures of Darwin’s Evolutionary Rhetoric,” 45. For example, Darwin wrote, “Slow though the process of selection may be, if feeble man can do much by his powers of artificial selection, I can see no limit to the amount of change, to the beauty and infinite complexity of the co-adaptations between all organic beings, one with another and with their physical conditions of life, which may be effected in the long course of time by nature’s power of selection.” Darwin, “The Origin of Species by Means of Natural Selection,” 109.

<sup>115</sup> Abeles, “The Agricultural Figures of Darwin’s Evolutionary Rhetoric,” 49.

crossing and inbreeding, instead emphasizing the power of selection of incremental improvements.<sup>116</sup> Theunissen suggests that Darwin's argument was somewhat arbitrary in that he modeled breeding on the practices of *pigeon fanciers*. Darwin himself reported that when a fancier suggested crossing at a meeting, the others displayed "solemn, mysterious & awful shakes of the head." Had Darwin instead chosen to study and theorize the practices of livestock breeders, focused on utility, he may have witnessed more crossing (as with Thoroughbreds) and inbreeding (as suggested by Bakewell).<sup>117</sup> Breeding, in practice and in theory, was complex and consensus rare. Despite his brief stint at breeding pigeons, Darwin had to rely upon the expertise and testimony of breeders, the "sloppy technicians," much of which was contradictory.<sup>118</sup> The pigeon fanciers' emphasis on purity prevented them from crossing, and thus, Darwin's theory downplays these mechanisms.<sup>119</sup>

If Theunissen is correct, this shows further how capitalism shaped Darwinism. Scholars now emphasize, especially in pedagogy, how the theories of political economist Thomas Malthus provided Darwin the key to how (artificial) selection would operate in the wild through the struggle for existence. As Marx commented to Engels, "It is remarkable how among beasts and plants Darwin recognises his English society with its division of labour, competition, opening up of new markets, 'inventions' and Malthusian 'struggle for existence.'" I argue that an extension of this recognition is that the phenomenon of systematic breeding as developed during the British Agricultural Revolution *equally shapes* the social context from which Darwinism emerged, as well as its very content. This is amplified by the [possibility] that the content of Darwin's theory of natural selection is a transference of not breeding in general, but pigeon fancying, an

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<sup>116</sup> By the publication of *Variation of Animals and Plants under Domestication* (1868), Darwin allowed for some crossing to explain the existence of some domesticated breeds, but its power and ubiquity remained subservient to artificial selection. Inbreeding remained inconsequential. Theunissen, "Darwin and His Pigeons. The Analogy Between Artificial and Natural Selection Revisited," 198–99.

<sup>117</sup> But Theunissen suggests that breeding culture became obsessed with "purity" (as seen in stud books), thus causing some breeders to downplay the importance of crossing, which "contaminated" the breed. Theunissen, 201, 204–5.

<sup>118</sup> Theunissen, 195. Theunissen suggests that Darwin focused on animals, not plants, because "most of his readers were familiar with the (mostly ordinary) domestic breeds he mentioned, whereas the countless varieties of cultivated plants were known only to specialists. Darwin considered his views to be equally valid for animals and plants though." Theunissen, 183.

<sup>119</sup> Darwin quoted in Theunissen, "Darwin and His Pigeons. The Analogy Between Artificial and Natural Selection Revisited," 192, 196.

amateur and cultural practice, in particular. Therefore, breeding, the active transformation of animals and plants, should at minimum be considered not simply as one of Darwin's lines of evidence, but as a *social and cultural determinant* of his theory, equal with Malthus and the *Beagle* voyage. Darwin attests to this when he wrote regarding selection in the margins of Youatt's cattle-breeding manual: "As this simple principle only lately discovered even in most valuable practice, no wonder not discovered, as theory of Species."<sup>120</sup> No capitalism, no Darwinian theory of evolution by natural selection.

Indeed, considering Wallace's role bolsters this argument of a fuller capitalist influence on Darwin's theory of evolution. In *Darwin Deleted*, Peter J. Bowler uses a counterfactual historical analysis to inquire about the history of evolution in Darwin's absence, requiring an analysis of Wallace's contributions. Bowler notes that the historical consensus states that while similar, Wallace's theory of selection (importantly, he did not use the term "natural selection") was more group-based against a static environment than Darwin's individual-based competition theory of selection. There are two key social-theoretical reasons for these differences: one, Wallace rejected comparisons between domesticated varieties and wild species, so Darwin's personal attention to this capitalistic phenomenon left its stamp on his theory, but not Wallace's. Second, Wallace's personal radicalism meant he tended to downplay competition, individualism, and parasitism in favor of emphasis on cooperative groups. His spiritualist views also grated against Darwin's materialism, leading him to adopt idealist tendencies such as mind-body dualism.<sup>121</sup> That is, Wallace forsook comparisons to the trove of results produced by the labor of breeders that Darwin treated as a form of experimental data, resulting in a theory that did not mesh with Darwin's worldview. This places Wallace outside the history of experimental evolution, or to some extent, places him as a critic.<sup>122</sup> But it also places capitalism as a necessary condition for Darwin's specific theory in the first place.

As I will show, much the same could be said of Mendel, and indeed, my dissertation

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<sup>120</sup> Abeles, "The Agricultural Figures of Darwin's Evolutionary Rhetoric," p 55.

<sup>121</sup> In addition, Bowler notes, Wallace being poor, relatively unknown, and remote (in order to make a living) contrasts with Darwin's well-known and well-connected bourgeois background — if there were no Darwin with whom to publish a joint paper, how could Wallace be taken seriously? Peter J. Bowler, *Darwin Deleted: Imagining a World without Darwin* (Chicago, Ill.: The University of Chicago Press, 2013), 60–66.

<sup>122</sup> This is not to say that Wallace was not positively impacted by capitalism, e.g., the reason he was in the Malay Archipelago in the first place was a way for him to engage in naturalist work while being paid — collecting animals to sell to the collectors and museums.

will show how practice, theory, and capitalism became more intertwined with evolution via breeding and experimentation, particularly as scientists became far more interested than Darwin in taking control of the process itself, a focus that began with Mendel.

### Gregor Mendel, Breeding Modeler

It is no coincidence that a Moravian monk was the figure to discover the laws of inheritance, for historians have revealed this region was also a thriving center of systematic breeding. Moravia had established a thriving community of natural scientists and agriculturists tied together by societies, professorships, journals and even monasteries.<sup>123</sup> Thus, both founding figures of modern evolutionary science were firmly embedded within cultures that valued the art of breeding, the *de facto* control of evolution, as a method by which to understand how nature operated. Unlike Darwin, however, Mendel set himself the task of understanding and modeling, by direct experimentation, what he later said in his famous paper was the “*transformation of one species into another through artificial fertilisation.*”

Reflecting the economic interests of Moravia, scientifically-minded breeders focused primarily upon sheep and plants. Ferdinand Geisslern, for example, had adopted Bakewell’s methods of combining crossing, inbreeding, and selection as well as conducting progeny tests. His methods and his farm, reminiscent of Dishley Grange, led him to become known as the “Moravian Bakewell.”<sup>124</sup> Cyril Napp, Mendel’s later abbot, was a fruit breeder who served as the president of the Brno Pomological Society, writing handbooks for local orchardists and establishing a nursery described as an “institute created for practical experiments.”<sup>125</sup> The Moravian breeders, who did not share Bakewell’s secrecy, were keen to elucidate practical scientific principles, circulating and debating their ideas through forums such as the Sheep Breeders’ Society.<sup>126</sup> This culture of exchanging theory and practice made Moravia a breeding capital.

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<sup>123</sup> Vítězslav Orel, *Gregor Mendel: The First Geneticist*, trans. Stephen Finn (Oxford: Oxford University Press, 1996), Chapter 2.

<sup>124</sup> Wood and Orel, *Genetic Prehistory in Selective Breeding: A Prelude to Mendel*, 192.

<sup>125</sup> Orel, *Gregor Mendel: The First Geneticist*, 23–24.

<sup>126</sup> For information on these interactions, see Wood and Orel, *Genetic Prehistory in Selective Breeding: A Prelude to Mendel*, 230–39. Curiously, while Mendel would not use the word “genetics” in his work, figures involved with the Sheep Breeders’ Society referred to “genetic laws of Nature” (“genetische Gesetze der Natur”) and “genetic forces.”

For the Moravians, natural history included agriculture. M. K. Fraas, a professor of agricultural botany, submitted a history to the Moravian Society for the Improvement of Agriculture, Natural Science, and Knowledge. Reminiscent of Darwin's "experiment on a gigantic scale," he wrote:

The fact that agriculture represents a summary of natural scientific experiments, governed by national economic priorities, is not generally understood. The results of experiments in open fields mean little to the pure naturalist. In contrast, we take it as axiomatic in the history of agriculture that it is fully competent to bring about scientific progress.<sup>127</sup>

Through this culture, Mendel was directly influenced by the tradition of plant breeders, particularly the hybridists Kölreuter and von Gärtner, whose problematic he took on himself.<sup>128</sup> Vítězslav Orel describes Joseph Gottlieb Kölreuter (1733–1806) as "the first pure naturalist to carry out systematic experiments with plant hybridization."<sup>129</sup> This was not only to understand the phenomenon; he imagined, for example, that it could be possible to produce a tree that grew at double the rate for the purpose of increasing timber production.<sup>130</sup> Karl Friedrich von Gärtner (1772–1850), who conducted his work to win a prize issued by a Dutch academy of science to confirm Kölreuter's discovery, performed "over 10,000 artificial fertilizations in 700 plant species, yielding 250 different hybrids," publishing his work in 1849.<sup>131</sup> Not only was Mendel heir to a tradition of experimental breeding, their work sparked a debate that Mendel specifically addressed: did hybridization show the generation of new species or, as Kölreuter and Gärtner thought, did it show that species were constant? While his experimental work is frequently described as about inheritance, this motivating question was about transformation, control and evolution – experimental evolution.

Unlike Darwin, who interpreted the "experimental" results of breeders, Mendel conducted evolutionary experiments himself. He was not interested in natural selection, though, and not narrowly in heredity, but in hybridization, reflecting his botanical

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<sup>127</sup> Quoted by Wood and Orel, 254.

<sup>128</sup> Mendel was also shaped by his academic experiences with physics and mathematics, as discussed by Robert Olby, *Origins of Mendelism* (London: Constable, 1966).

<sup>129</sup> Orel, *Gregor Mendel: The First Geneticist*, 17.

<sup>130</sup> Orel, 17.

<sup>131</sup> Orel, 11–12.

focus.<sup>132</sup> Thus, like Darwin, Mendel's work follows a specific tradition of breeding. Mendel described his findings *not* as the "laws of inheritance" (as we do today), but as a "generally standard law for the *formation and development of hybrids*."<sup>133</sup> This was to explain why "the same hybrid forms reappeared whenever fertilisation took place between the same species."<sup>134</sup> Kölreuter's and Gärtner's experiments on "artificial fertilisations of ornamental plants to produce new color variants" were his inspiration. Mendel's concluding remarks revealed that he discovered his so-called laws of inheritance by pursuing a statistical model to explain the conflicting results regarding the "*transformation of one species into another through artificial fertilisation*."<sup>135</sup>

Before describing his experiments, Mendel justified his experimental system: peas in a garden.<sup>136</sup> For his choice of plant, he had three criteria. The first, "possess[ion of] constantly differing characters," eased analysis. The second, a shield to prevent unintentional pollination by neighboring plants, and the third, steady hybrid fertility, minimized environmental influences.<sup>137</sup> After selecting the plant genus *Pisum*, he conducted an experimental control through a two-year trial to confirm that his seeds bred true to type. To justify an extrapolation from domesticated peas to other organisms, he appealed to evolution:

One might well suppose that for important points a fundamental difference cannot occur [between species] since the unity of the evolutionary plan of organic life is beyond question.<sup>138</sup>

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<sup>132</sup> Mendel's focus on hybridization as opposed to selection perhaps reflects Mendel's following of Kölreuter and Gärtner, rather than Moravian sheep breeders who focused on artificial selection.

<sup>133</sup> Emphasis mine.

<sup>134</sup> Scott Abbott and Daniel J. Fairbanks, "Experiments on Plant Hybrids by Gregor Mendel," *Genetics* 204, no. 2 (2016): 407.

<sup>135</sup> Abbott and Fairbanks, 421. Italics original. The usage of "species" probably makes this sound starker than what Mendel meant: We would use "varieties" to describe the different forms of Mendel's plants. (Even if we interpreted them as different species, these hybridizations were within the genus *Pisum*.) Mendel considered the distinction between species and variety "completely unimportant" for the purpose of his experiment. In his conclusion, Mendel tentatively held that species have fixed limits; thus, this method was not a source of unlimited creation.

<sup>136</sup> For this discussion, I am exclusively relying upon Mendel's paper as published, rather than discussing the work as it historically occurred.

<sup>137</sup> Abbott and Fairbanks, 408. The Mendelians would later argue that the first criterion, with an emphasis on choosing discontinuous characters, also ensured that environmentally-caused variations were not confused for hereditary ones.

<sup>138</sup> Ibid., 421.

Mendel echoed Darwin and Fraas when minimizing the distinctions between the garden and the “natural landscape.” He scoffed, “no one will seriously assert that the development of plants in a natural landscape is governed by different laws than in a garden bed.”<sup>139</sup> However, the use of a cultivated plant, when combined with the garden bed, generated a further complication he had to address. Recall that Wallace and Lyell had opposed Darwin’s use of domesticated livestock on the grounds that domesticates, by virtue of their environmental history, were more variable than their wild counterparts, and thus too artificial to serve as parallels to biological evolution.<sup>140</sup> Mendel interpreted this trend of “opinion” as holding “that the stability of a species has been disrupted to a high degree or utterly broken through cultivation.” He suggested that this belief implied that “the development of cultivated forms ... proceed[s] without rules and by chance.”<sup>141</sup> Mendel’s research would provide these rules, but he had to account for this opinion; in fact, he believed his laws demonstrated that this difference between wild and cultivated was not one of *kind*, but one of *degree*.

Mendel wrote,

It is not apparent, however, why the mere placement in garden soil should result in such a drastic and persistent revolution in the plant organism. ... Here, just as there [in the “natural landscape”], typical variations must appear if the conditions of life are changed for a species, and it has the ability to adapt to the new conditions. It is freely admitted, through cultivation the production of new varieties is favoured, and by the hand of man many a variation is preserved that would have failed in the wild state, but nothing gives us the right to assume that the tendency for new varieties to form is so extremely augmented that species soon lose all stability and that their offspring break up into an infinite array of highly variable forms.<sup>142</sup>

Mendel argued similarly to Darwin’s use of metonymy: the results may differ between “Man” and “nature,” but the processes of variation and heredity remain the same. Thus, according to Mendel, the garden and the wild did not operate under different laws; the

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<sup>139</sup> Ibid., 418.

<sup>140</sup> Inkpen, “Denaturing Nature.”

<sup>141</sup> Abbott and Fairbanks, “Experiments on Plant Hybrids by Gregor Mendel,” 418.

<sup>142</sup> Abbott and Fairbanks, 417–18. Emphasis mine. Abbott and Fairbanks single this paragraph out as being especially influenced by Darwin. See Daniel J. Fairbanks and Scott Abbott, “Darwin’s Influence on Mendel: Evidence from a New Translation of Mendel’s Paper,” *Genetics* 204, no. 2 (2016): 403–4.

production of variation and the “ability to adapt” were the same in both sites. The difference was that in the garden, breeders encouraged variations to persist that nature by itself would never allow.<sup>143</sup>

Mendel also countered the Wallacean trend by emphasizing the importance of internal factors. He pointed out that if “the change in the conditions of vegetation were the sole cause of variability,” then plants “cultivated under almost the same conditions for centuries would have acquired stability.”<sup>144</sup> But, acquired stability is not the case, because such plants continued to produce new varieties; thus, he argued, *there is something internal*.

That there were internal laws to species was exactly what Mendel demonstrated through his model of hybridization. Following his experiments, Mendel believed he could explain hybridity’s apparent contradictions discovered by Kölreuter and von Gärtner through mathematical rules. For example, a hybrid sometimes resembled one parent more than the other; Mendel explained this as one parent having more dominant characters than the other. Additionally, statistical reasoning dictated that an incredible number of individuals were required to detect inherited patterns — “for seven different characters” the two parents would “reappear” only twice among 16,000 offspring.<sup>145</sup>

Mendel’s theory also explained the variable results reported by his predecessors regarding “artificial transformation.” What they ascribed to vague differences in “vigour” or type, Mendel explained with dominance and recessiveness. In fact, his laws provided a model by which to predict the speed of transformation. Kölreuter and von Gärtner had developed a method, “the most difficult in the production of hybrids”: If one took Plant A and wished to transform it into Plant B, a series of hybridizations between Plant A-B hybrids with Plant B’s pollen could eventually effect the transformation. The number of generations is what had confused them. Mendel explained their troubles: Longer transformations were due to a higher “number of differing characters” and a low “number of experimental plants.” For three differentiating characters, in which Parent A was

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<sup>143</sup> A difference that Hugo de Vries would emphasize is differences in nutrition, which he considered to be a notable influence in evolution.

<sup>144</sup> Abbott and Fairbanks, “Experiments on Plant Hybrids by Gregor Mendel,” 419. While the Mendelians would argue that “changes in the conditions of life” were not a major cause of variability, Mendel — like Darwin — did.

<sup>145</sup> Abbott and Fairbanks, “Experiments on Plant Hybrids by Gregor Mendel,” 419–20.



dominant (*AABBCC*) and B recessive (*aabbcc*), F<sub>1</sub> hybrids would be identical (*AaBbCc*) but produce eight different gametes, only one of which would contain all three recessive characters (*abc*); thus, a cross between A-B and B would reproduce B in 1/8 of the offspring. If the number of offspring was too low, B might not appear at all; but, if one isolated the closest combinations, in which two characters were the same as B (recessive) (e.g., *aaBbcc*), and cross again, the F<sub>3</sub> generation would reproduce B in half of the offspring (*aaBbcc* and *aabbcc*). The following generation could give B permanently.

Following the modernized interpretations of Hartl and Orel, these “transformed” hybrids were “constant hybrids,” which propagated offspring true to their type when crossed (because they were homozygous). They could be broken again, however, if crossed with a different form. What von Gärtner and Mendel labeled “transformation,” geneticists may see as a mere extraction of a type from a hybrid, or a backcross (a common method in *Drosophila* genetics). That this was considered such an important problem highlights how different pre-Mendelian theories of heredity were to modern ones, where the goal, transformation, has become a mere technique, the backcross.

Thus, Mendel had devised a model by which variation in “artificial transformation” could be explained, if not predicted, reflecting a practical bent to his research.<sup>146</sup> As with Darwin and with other Moravian breeders and academics, Mendel deployed artificial experimentation to understand both nature and artifice and to develop practice into theory. Because of his interest in hybridization, development, and evolution, I argue that Mendel’s landmark work can be considered an early episode of experimental evolution — even though natural selection had no place in it. By minimizing the distinction between the artificial and the natural, with regard to both *organisms*, via their evolutionary history and proper environmental controls, and *site*, via the universality of scientific law, Mendel helped lay down the foundations for an experimental biology — genetics and experimental evolution. From its very foundation, Mendel’s genetics intertwined theory with practice, a practice grounded in the capitalist social relations that gave rise to the modern methods and culture of breeding. In contrast to Darwin’s theory, however, Mendel’s was less capitalist in content. Mendel did not produce or envision a theory as all-encompassing as Darwin and he did not have the time to do so. (Although

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<sup>146</sup> Abbott and Fairbanks, 421–22.

notably when he became abbot he remained active in agricultural and plant-breeding societies and even experimented with bees.<sup>147</sup>) There was not obvious room to incorporate the thought of political economy in a model that explained color inheritance in pea plants, at least not immediately. The further integration between theory and practice, science and society, had to wait for Mendel's rediscovery in 1900.

### **Toward Making Evolution Visible: Reverend William Dallinger**

While Mendel focused on hybridization and “artificial transformation,” the first explicit selection experiment, strangely enough, was conducted upon microbes in England. In the 1870s, Wesleyan Reverend William Henry Dallinger (1839-1909) sought to test the fact of organic change and constructed an incubator specific to the job.<sup>148</sup> By slowly increasing the incubator's temperature over several years, Dallinger forced protists to adapt to an environment of his own making.<sup>149</sup> In contrast to Darwin's use of breeding as an experiment, Dallinger designed, constructed, and conducted the experiment himself with the intention of demonstrating a hypothesis — evolution by natural selection —, thus providing a “first” for experimental evolution, showing both its promises although moreso its difficulties.

William Dallinger was part of the nineteenth-century tradition of parson-naturalists, Darwin's destiny had he not boarded the H.M.S. Beagle. Focusing on the microscopical study of microbial life, Dallinger dedicated his scientific research to the intertwined debates over spontaneous generation and Darwin's theory of evolution by natural selection.<sup>150</sup> His scientific views were unusual from the perspective of both Wesleyanism and microbiology. Many microbiologists, led by Louis Pasteur, rejected spontaneous generation, but due to a perception that Darwinism rested upon spontaneous generation, they also rejected Darwinism. With respect to religion, while Methodists and

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<sup>147</sup> Orel, *Gregor Mendel: The First Geneticist*, 219–42.

<sup>148</sup> J. W. Haas, Jr., “The Rev. Dr. William H. Dallinger F. R. S.: Early Advocate of Theistic Evolution and Foe of Spontaneous Generation,” *Perspectives on Science and Christian Faith* 52 (2000): 107–17.

<sup>149</sup> “Protists” is not a term that Dallinger would have used. Neither was “microbe.” He described his organisms as “monads” and “infusoria.” Because I am not focusing on microbiology, I see no need to restrict myself from using more familiar terms.

<sup>150</sup> Like Darwin, the financial stability required for this lifestyle was achieved through marriage. Haas, Jr., “The Rev. Dr. William H. Dallinger F. R. S.: Early Advocate of Theistic Evolution and Foe of Spontaneous Generation,” 108.

Wesleyans had positive views of science, they initially rejected Darwin's theory.<sup>151</sup> That Dallinger devoted his scientific career to studying microbes while rejecting spontaneous generation *and* supporting Darwin makes him unusual.

Dallinger's views and research, however, did align him with the X Club, a small cadre of scientists (including T. H. Huxley and John Tyndall) whose goal, among others, was to establish Darwinism in English science. Among their goals was to decouple Darwinism from spontaneous generation, primarily by eliminating the latter as a legitimate scientific theory.<sup>152</sup> Dallinger's work on microbes, therefore, supported the Darwinian cause. By closely tracking the life cycle of "monads," Dallinger concluded, along with a collaborator, James Drysdale (who could observe the organisms while Dallinger slept), that small spores did not spontaneously arise, but originated from larger monads. Their work became a weapon for the X Club, especially for Tyndall, who personally encouraged Dallinger and cited him in public lectures.<sup>153</sup> Haas, Jr., the only author to treat Dallinger in a historical context, concludes, "Dallinger had been used by his X-club friends to furthering their campaign from the question of the origin of life. In turn, he used their patronage to carve out a scientific niche based on his meticulous work in microbiology."<sup>154</sup>

Following his research on monad life-cycles, Dallinger turned toward an experimental demonstration of Darwinism. As Dallinger later reported in his 1886 presidential address to the Royal Microscopical Society, he sought to discover "whether it was possible by change of environment, in minute life-forms, whose life-cycle was relatively soon completed, to superinduce changes of an adaptive character, if the

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<sup>151</sup> Haas, Jr., 110–12. Wesleyan rejection of Darwinism appears primarily to have been on moral grounds. Unfortunately, we do not know why Dallinger accepted Darwinism. From 1877 to 1902, he wrote about science for the *Wesleyan Methodist Magazine*, possibly contributing to the sect's growing acceptance of the theory.

<sup>152</sup> James Edgar Strick, *Sparks of Life: Darwinism and the Victorian Debates over Spontaneous Generation* (Cambridge, Mass.: Harvard University Press, 2000). Maureen O'Malley has also shown that Darwin did the same in the third edition of *The Origin*: He distanced himself from Lamarck's theory in that it rested upon "the spontaneous generation of simple life-forms that make evolutionary progress into complex ones." Maureen A. O'Malley, "What Did Darwin Say about Microbes, and How Did Microbiology Respond?," *Trends in Microbiology* 17, no. 8 (2009): 343.

<sup>153</sup> J. W. Haas, Jr., "The Reverend Dr William Henry Dallinger, FRS (1839-1909)," *Notes and Records of the Royal Society* 54, no. 1 (2000): 58–59.

<sup>154</sup> Haas, Jr., 56.

observations extended over a sufficiently long period.”<sup>155</sup> Dallinger personally saw no need for “direct demonstration” of Darwin’s theory. To him, it “underlies as a necessity all our widest and deepest biological knowledge” and that “concurrent adaptation to concurrent changes of environment is in fact so apparent now, that we wonder, often, why it was not earlier seen.”<sup>156</sup> Still, experimentally demonstrating the truth of natural selection “cannot be other than a gain both to philosophical and practical biology.”<sup>157</sup>

Dallinger meticulously conducted a year-and-a-half long trial, concluding that the monads from the life-cycle studies were optimal for the experiment. From his experiment investigating the “death point” of monads, he found that “the best and most amenable agent ... for altering slowly and cumulatively the environment, was heat.”<sup>158</sup> Dallinger communicated his preliminary findings to Darwin, who responded,

I did not know that you were attending to the mutation of the lower organisms under changed conditions of life; and your results, I have no doubt, will be extremely curious and valuable. The fact which you mention about their being adapted to certain temperatures, but becoming gradually accustomed to much higher ones is very remarkable.

Ever the naturalist, Darwin continued, “it explains the existence of algae in hot springs. How extremely interesting an examination under high powers on the spot, of the mud of such springs would be.”<sup>159</sup>

Following Darwin’s theories, Dallinger emphasized the “smallness of every variation.” Normally imperceptible, it was only Darwin’s own emphasis on domestication as an agent of evolutionary change that “made clear” “the great process of biological progression.”<sup>160</sup> Likening biology to another historical science — astronomy, in which

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<sup>155</sup> William H. Dallinger, “President’s Address,” *Journal of the Royal Microscopical Society* 7, no. 2 (1887): 191.

<sup>156</sup> He further claimed that “variations are constant, of that there can be no doubt” (p. 192).

<sup>157</sup> *Ibid.*, 191. By “practical biology,” Dallinger meant experimental biology.

<sup>158</sup> *Ibid.*, 191.

<sup>159</sup> Quoted in Dallinger, “President’s Address,” 1887, 191–92. Charles Darwin, “To Dallinger, W. H.,” July 2, 1878, <https://www.darwinproject.ac.uk/letter/?docId=letters/DCP-LETT-11587.xml>, accessed on 15 May 2021. Dallinger and Darwin had corresponded briefly previously, in which Darwin lauded the work of Dallinger and Drysdale on microbial life-cycles and spontaneous generation. Haas, Jr., “The Rev. Dr. William H. Dallinger F. R. S.: Early Advocate of Theistic Evolution and Foe of Spontaneous Generation,” 112.

<sup>160</sup> Dallinger, “President’s Address,” 1887, 192.

observations of “a minute fraction of the complete cycle of movement, leaves us ... certain” of the entire cycle — Dallinger thought “any observed facts that may come within our reach, or be possible to our laboratories, [are] of even enhanced value.”<sup>161</sup> Thus, a laboratory experiment of natural selection in action was legitimate and useful. However, an adherence to gradualism ruled out plants and animals, whose complexity and “relative fewness of generations” would prevent the observation of evolutionary changes “during the working life of an observer.” Thus, only microbes allowed evolution to be made visible. To justify these organisms as legitimate objects of evolutionary study, Dallinger reminded his audience that all organisms are composed of cells.

Once he finished his preliminary experiments, Dallinger ordered a customized thermostatic incubator outfitted with a mercury regulator that allowed water in three glass chambers to be kept indefinitely at steady temperatures, but also raised and lowered at will.<sup>162</sup> (See Figure 1.)

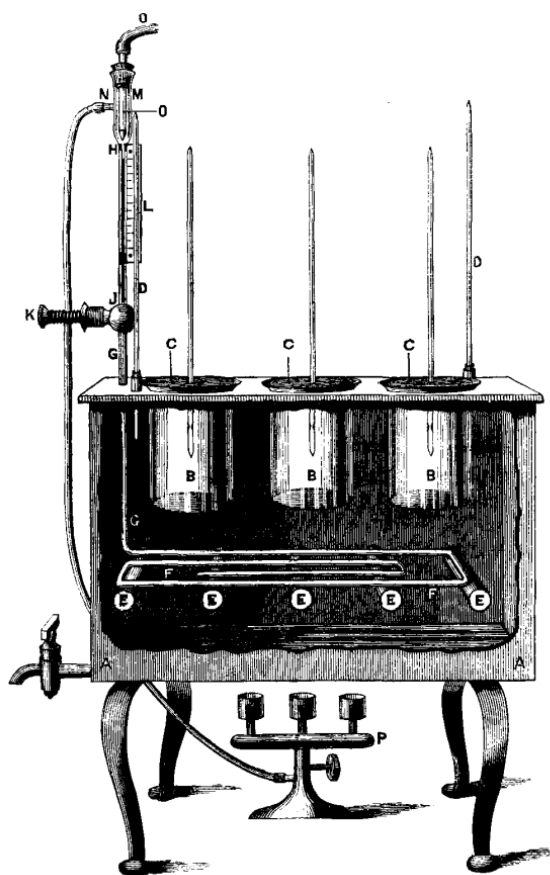


Figure 1. From Dallinger, “President’s Address,” *Journal of the Royal Microscopical Society* 7, no. 2 (1887), 193.

<sup>161</sup> Dallinger, 192.

<sup>162</sup> Dallinger, 193–95. See Appendix A for a description of how the instrument worked. William H. Dallinger, “Dr. Dallinger’s Thermostatic Continuous Stage,” *Journal of the Royal Microscopical Society* 7, no. 2 (1887): 317–18. Dallinger had initially constructed a similar apparatus for the purpose of studying a “septic organism” at its normal temperature, 90–95° F. For an interesting discussion of the instrument, see Sheref Mansy and Sascha Pohflepp, “Living Machines,” in *Synthetic Aesthetics: Investigating Synthetic Biology’s Designs on Nature*, ed. Alexandra Daisy Ginsberg et al. (Cambridge, Mass: The MIT Press, 2014), 247–58.

For seven years, Dallinger slowly and meticulously raised the temperature of his instrument from 60° F., where the three microbial species (*Monas Dallingeri*, *Dallingeria Drysdali*, and *Tetramitus rostratus*) could thrive, all the way up to 158° F.<sup>163</sup> This was not a smooth increase, however; after an increase of a few degrees, continued adaptation paused — once for up to twelve months (from 137° to 138° F.). Dallinger noticed that at each pause, the monads would “vacuolate,” in which internal empty chambers grew within the cell, and “the vital vigour and all the vital activities of the organisms ... regained.”<sup>164</sup> Dallinger never postulated a reason for this change. He did observe that when these vacuoles disappeared, the microbes became adaptable to further temperature increases. He noticed no morphological or behavioral changes.

When Dallinger’s incubator reached 158°, “the accident happened, destroying the use of the instrument, and causing the whole to collapse.”<sup>165</sup> Dallinger concluded from his long experiment:

... There seems to be indicated in these observations, as imperfect as they are, that there is at certain points in the endurance of cumulative thermal elevations, a distinct physiological change brought about with greater or less difficulty, which seems to be directly correlated to the power of adaptation to a given measure of heat increment. It is not a quiet rhythmic progression. There are points of greater and of less difficulty.<sup>166</sup>

Cautious, Dallinger recognized the artificiality of his experimental system. Perhaps referencing Darwin’s comments to him about algae, Dallinger prefaced this conclusion that he “did not succeed in raising the temperature in these forms to anything like the elevations that the algae and other low forms have been found in nature to flourish in.” Furthermore, “I do not pretend to say, nor do I wish to draw any general inference as to even this *group* of organisms. My observations were only on these three special forms.”<sup>167</sup> Dallinger was wary to extrapolate beyond these specific organisms that

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<sup>163</sup> The organisms Dallinger used were *Tetramitus rostratus*, *Monas Dallingeri*, and *D. Drysdali*. The degree to which our named microbial species today match what was used by Dallinger and his contemporaries is unclear. For example, the genus *Monas* has mostly been dissolved, its species being dispersed throughout the protista. Jens Boenigk, “The Past and Present Classification Problem with Nanoflagellates Exemplified by the Genus *Monas*,” *Protist* 159, no. 2 (2008): 319–37.

<sup>164</sup> Dallinger, “President’s Address,” 1887, 196.

<sup>165</sup> Dallinger, 199.

<sup>166</sup> Dallinger, 199.

<sup>167</sup> Dallinger, 199 Emphasis original.

evolved in this specific instrument. Furthermore, he recognized the novelty generated by his experiment. He had evolved these three species of microbes to thrive in temperatures that would kill them normally, but if he placed the evolved populations into the original temperature, they, too, would die.<sup>168</sup> Although he did not say so explicitly, Dallinger had created a microbial form that had never before existed and that no longer existed after the experiment.

What Dallinger's address left unclear was the "method" by which this adaptation was produced; however, in an 1887 published lecture, *The Creator, and What We May Know of the Method of Creation*, Dallinger pointed to natural selection. Citing his experiment, he continued to use "adaptation," but on the following page, he cited and summarized Darwin's theory of natural selection and wrote, "it is impossible for a biologist to withhold consent to the fact that a 'law,' a method, has been demonstrated, which has been a certain and powerful factor." Furthermore, "that there are other factors of evolution not yet discovered is almost inevitable; they, however, will be but added 'laws.'"<sup>169</sup> Given this strong endorsement of natural selection at a time in which it was not well-accepted, I am inclined to think Dallinger thought he had demonstrated not only evolution and adaptation, but natural selection specifically.<sup>170</sup>

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<sup>168</sup> Dallinger, 199.

<sup>169</sup> William Henry Dallinger, *The Creator, and What We May Know of the Method of Creation* (T. Woolmer, 1887), 69–70. Dallinger's address is an argument for natural theology in the wake of major scientific developments, specifically reconciling his work on spontaneous generation and evolution with a Creator God. He argued that, contra Paley, there was no special creation — either of species or of life; instead, he thought God endowed the universe with laws (e.g., gravity and natural selection) at the beginning of time. Scientists were thus revealing those laws and the "methods" by which God designed the universe. He rejected Ernst Haeckel's reduction of protoplasm to simple albumen, i.e., that life was simply the congregation of complex molecules (pp. 34–35). Dallinger's primary target was Herbert Spencer's materialist philosophy which he argued could not explain much of anything, but especially mind and consciousness. He endorsed the evolution of humans, also, but thought it remained a mystery as to the "method" by which God "breathed into [Man's] nostrils the breath of life" (p. 81).

<sup>170</sup> However, Dallinger, like Asa Gray, was not fully on board with Darwin's vision. To Dallinger, what Darwin left unexplained were the universal "laws" of variation and inheritance (pp. 69–74). He wrote, "An equally powerful weapon in defence of theism takes its place: I designate it 'CONCURRENT ADAPTATION;' that is, fitness, for ever, throughout all time and all space; and fitness absolutely constant amidst all changes. Adaptation is universally concurrent with existence; and whether we have to account for it by sudden and unexplained action, or by the slow operation of laws, is a matter of no essential moment: it is there" (p. 72). Recapitulating Darwin's instances of orchid-insect coevolution, what "this great biological law affirms, is, that whatever the changes, and however brought about, past or future, there never has been, there is not, and there never will be, an instant's cessation of concurrent adaptation: — the operation of the 'law' that secures to all that lives adjustment to its environments" (p. 74). Thus, natural selection, like gravity and matter, had its origins in the Creator when he set forth the laws of the universe upon its creation: "That surely must be a method that took its origin in mind; and it must have had its

As unique as Dallinger's evolution experiment was for the time, he never published the results beyond this address. In fact, he ceased most research on microbes, although it is clear he paid close attention to developments in the field. In 1892 and 1893, for example, he lectured as president to the Quekett Microscopical Club, mostly updating members on recent developments in microscopy and microbiology. In 1892, he discussed extensively the pathological role bacteria play as emphasized by Pasteur and Koch.

In these lectures, Dallinger suggested further conclusions that he did not include in his initial 1887 address. He noted that he began his evolution research before Pasteur, so that his results are not directly relevant to research on pathogenic bacteria; however, he did make a case for comparison. He claimed his research had shown that microbes, "in less than ten years," can be "trained by prolonged and cumulative change of environment" "to live, even with increased fecundity" at temperatures nearly 100° F. higher than normal. He pointed out that he observed not morphological changes, but physiological changes — "simply a modification of function."<sup>171</sup> Therefore,

it is physiologically and not morphologically that the saprophytes are subject to mutation, so much so that unless we take a very broad and philosophical view of what is specific, we may even appear to approach by such mutation a physiological specificity concurrently with a morphological identity with unaltered forms. The remarkable morphological similarity of certain bacilli, whose physiological differences are terribly unlike, must strike a very casual observer.<sup>172</sup>

Here Dallinger speculated that the defining characteristic of microbes was not their shape, size, or form, but their physiology and function. In fact, he thought morphological identity could mask physiological evolution, especially because his experiments demonstrated how quickly these microbes could evolve.

How far may these [physiological changes], if constantly taking place in nature, at times fill the air with minute organisms in vast clouds, which by certain altered conditions have become endowed with functional characters inimical to man and beast, taking for a time the place of common forms with which the air is usually charged, but as a rule innocuous

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prevised and pre-ordered place potentially assigned, from the earliest creative moment" (p. 74). For more on the acceptance of Darwinism, see Peter J. Bowler, *The Non-Darwinian Revolution: Reinterpreting a Historical Myth* (Baltimore: The Johns Hopkins University Press, 1988).

<sup>171</sup> William H. Dallinger, "President's Address," *Journal of the Quekett Microscopical Club* 5 (1893): 42.

<sup>172</sup> Dallinger, 43.



to man and beast?<sup>173</sup>

He concluded, “I venture to believe that the question of the functional mutability of these organisms and its causes and consequences will form some considerable portion of the work of the next quarter of a century.”<sup>174</sup>

However, he was not to take part. As Haas, Jr. points out, Dallinger wrote in his address that because his study of saprophytic microbes had led him “to the very edge of pathological inquiry, I was obliged to leave it there, having neither special medical training nor proper opportunity for its further pursuit on the pathogenic side.”<sup>175</sup> He thus lamented the professionalization of science that had taken place during his lifetime, causing him to wonder what role amateurs like him could play. Although in 1892 he indicated that he had an ongoing evolution experiment, he never published results. In his 1893 address, he critiqued O. Bütschli’s work on the artificial generation of protoplasm and discussed positively Sergei Winogradsky’s discovery of the bacterial role in soil nitrification, but he reported no research of his own. Instead, Dallinger focused on the microscope itself, writing and publishing a revamped edition of William B. Carpenter’s *The Microscope and Its Revelations*, his last scientific contribution before his death in 1909.

Dallinger’s experiment is noteworthy for a number of reasons. He is likely the first scientist, besides Mendel, to whom we can attribute the term “experimental evolution,” and the first to conduct a selection experiment, for he worked within a modern evolutionary framework and utilized an evolutionary force — natural selection — over many generations. From a historical perspective, what makes Dallinger’s experiment of such interest, beyond it merely being “the first” scientific selection experiment, is how well it captures aspects that characterize all of experimental evolution, then and now. Dallinger was not an evolutionary scientist — at least to the degree that such a person existed in the nineteenth century —, but an amateur parson-naturalist studying microbes, a predecessor to the bacteriologist, and later, the microbiologist. He dedicated most of his scientific research to refuting spontaneous

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<sup>173</sup> Dallinger, 43.

<sup>174</sup> Dallinger, 44.

<sup>175</sup> Dallinger, 39.

generation and developing the microscope, but for nearly a decade, he also conducted an evolutionary experiment on adaptation. Strikingly, the importance of instruments and systems built specifically for the problem at hand is already present in his work, something that would not resurface in experimental evolution until the 1930s (population cages) and the 1950s (chemostat). As with many later experimental evolutionists, he was careful about his experimental organism(s): they needed to be simple, manipulable, and quick to reproduce. However, unlike those who worked after him, his response to the artificial/natural distinction was to limit most of his conclusions to the system itself. Although he did conclude that evolution is not always a “quiet rhythmic progression,” but potentially a process of fits and starts, and warned of physiological changes in bacteria, he never put forward a general theory based on these claims. Another major difference between Dallinger’s experiments and those conducted by early twentieth-century biologists is that Dallinger had purely a research question at mind; he apparently envisioned no *practical* purpose beyond demonstrating the reality of evolution. But as a parson-naturalist he saw his work as part of a natural theology.

Despite Dallinger’s achievement, he had little influence on evolutionary research. Strangely, while scientists mentioned him a few times in the late nineteenth century, I have yet to find him cited by any early twentieth century experimental evolutionist; even stranger, he is cited today by twenty-first century biologists as a “father” to the field even though there is no genealogical connection. (What is important to today’s scientists is that he worked with microbes, not plants or animals.)<sup>176</sup> His colleagues did praise his work, however. See Appendix A2 for a discussion of reactions from his contemporaries and later nineteenth-century scientists.

Dallinger was not necessarily “ahead of his time.” His work bore the stamps of

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<sup>176</sup> Scientists also argue that Dallinger’s experimental success was due not to evolution, but to contamination. See Tadeusz J. Kawecki et al., “Experimental Evolution,” *Trends in Ecology & Evolution* 27, no. 10 (2012): 547–60; Theodore Garland and Michael R. Rose, eds., *Experimental Evolution: Concepts, Methods, and Applications of Selection Experiments* (Berkeley: University of California Press, 2009). Claudia Bank et al., “Thinking Too Positive? Revisiting Current Methods of Population Genetic Selection Inference,” *Trends in Genetics* 30, no. 12 (2014): 540–46; Rees Kassen and Paul B. Rainey, “The Ecology and Genetics of Microbial Diversity,” *Annual Review of Microbiology* 58, no. 1 (2004): 207–31. I am not sure if there exists a definitive solution to the dilemma, unless we know that such a stark adaptation is impossible. We do know that Dallinger was careful and rather observant, so if there was contamination, it is likely due to instrumentation not so much a failure in his character. The problem of contamination will surface again, specifically in my discussion of Hugo de Vries and William Tower.

nineteenth-century evolution and biology. He was contemporary with Louis Pasteur and other biologists who had begun to experimentalize the discipline and take microbes seriously as experimental subjects. In contrast to modern microbial experimental evolutionists, Dallinger did not employ his monads because of their astonishingly large population sizes; instead, he cited *only* simplicity and fast generation times. Furthermore, his results were depicted as drawings of idealized (“average”) individuals; no population indices were quantified or likely even considered. Instead, he was simply concerned with adaptiveness to temperature via morphological and visible physiological responses. Dallinger was thoroughly a naturalist of the nineteenth century. As experimental evolution took off in the early twentieth century, the complications of Dallinger’s experiments, as well as his focus on microbes and not plants and animals, likely contributed to his historical neglect. The first selection experiment was quite a spectacular achievement, despite its problems, but it apparently failed to capture the imagination of his immediate successors, waiting until the late twentieth century to be noticed once again.

### Conclusion

Experimentation was crucial to modern evolutionary science from its very inception; in fact, without experimentation, there would be no evolutionary biology as we know it today. While Darwin conducted experimental evolution in an unusual and indirect way, his reliance on the practice and experience of breeders was essential to forming his theory of evolution by natural selection. Darwin’s use of metonymy highlights what Marx and Engels saw as valuable in his work: he did not see a formal distinction between nature and artifice, as two unrelated spheres, but instead as two poles of opposition and interdependence, artifice as having emerged from nature itself. This transformation of nature had begun thousands of years prior, but what had changed was breeders’ conscious control of nature according to their desires (i.e., profit, in a capitalized system of agriculture) at a visible rate. This activity of transformation could now be theorized. As Bukharin wrote, “Practice is an active break-through into reality, egress beyond the limits of the subject, penetration into the object, the “humanising” of nature, its alteration.” That the “sciences ‘grow’ out of practice, the ‘production of ideas’

differentiates out of the ‘production of things.’”<sup>177</sup> That evolution is not immediately perceptible, but happens on the scale of generations, does not alter this core thesis, that “theory is accumulated and condensed practice.” Where Darwin further excelled beyond mere theorization of practice was to then, in combination with Malthus, argue that the practice of breeders also explained the unity and diversity of life through the wealth of facts accumulated by the disciplines of natural history.

Mendel forged a similar path through his work on “artificial transformation.” Considered somewhat of an outsider to the evolutionary tradition, requiring interpretation and synthesis, viewed his own project of understanding “artificial transformation” as part of the breeding agenda of Moravia, one similar to Darwin’s own, and not as simple “laws of inheritance.” He, too, saw his work in a universal way, challenging the notion that there were distinct laws governing cultivated plants in soil beds apart from wild plants in natural landscapes. He did not pursue his theories with the same verve as Darwin, but he did lay the groundwork for sweeping changes to both theory and practice when rediscovered decades later, especially when it his work was rechristened as “genetics.”

Dallinger, the first to conduct a long-term selection experiment, was far more reluctant to extrapolate his work to nature, instead emphasizing the artificiality of his work, in creating new forms in small volumes of hot water. Yet he had achieved the task (arguably, in retrospect) of rendering the normally imperceptible process of evolution *visible*, showing that there were ways to overcome Darwinian gradualism without resorting to “sloppy technicians” through dedication to long-term experimentation. Control and utility under scientific guidance would come later.

The question remains of the connections between this early work of experimental evolution to its later development. The tenuous and indirect connections were partially a result of a lack of institutionalization — Darwin, Mendel, and Dallinger did not launch experimental programs with established physical or social spaces (including journals) that could build a store of accumulated theory and practice. Furthermore, they were not professional scientists and the latter two especially did not share Darwin’s extensive

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<sup>177</sup> Nikolai Bukharin, “Theory and Practice from The Standpoint of Dialectical Materialism,” in *Science at the Crossroads: Papers Presented to the International Congress of the History of Science and Technology Held in London from June 29th to July 3rd, 1931 by the Delegates of the U.S.S.R* (Frank Cass and Co., 1931).

network and wealth to fund work that would make evolution visible, controllable, and useful. The realization of this need would emerge, but not before experimental evolution re-emerged on a stronger and professionally scientific basis and importantly as central to the debates that raged over the relationship between the two founding figures of evolutionary sciences, Darwin and Mendel, and critically over the debate's implications for the control of evolution. Thus, the history of experimental evolution must begin with Darwin and Mendel, *in combination* with the social relations of capitalism from which they emerged, of which I chose Robert Bakewell, an eighteenth-century English sheep breeder, as its personification.

## Chapter 2: Making Evolution Visible

### Introduction

Two biologists in particular took on experimental evolution in the late nineteenth century: English naturalist and statistician Walter Frank Raphael Weldon (1860–1906) and Dutch botanist Hugo de Vries (1848–1935).<sup>178</sup> They both shared a vision of making natural evolution visible, just as Dallinger had attempted, but proclaimed differing (but not mutually exclusive) programs to carry out the task. Weldon adopted (orthodox) Darwinian *theory*, and developed in collaboration with Karl Pearson the methods of biological statistics, biometry, to amass the data that could reveal *natural* selection in action. De Vries championed Darwinian *method*, relying upon experimentation, whilst developing a heterodox theory of evolution by mutation. (De Vries also argued that his theoretical ideas germinated from Darwin's thought.) They both thus claimed heritage of the Darwinian tradition, revealing its ambiguous meaning. But particularly crucial was that as much as Weldon wanted to avoid experimentation, his projects forced him to take it on. The first half of this chapter examines Weldon's non-experimentalist research program as it developed into experimental lines to answer the questions he had of evolution. This is an interesting case of theoretical commitments giving way to limitations it imposed upon practice. I then briefly address geneticist William Bateson's critique of biometry as it highlights the experimentalist ideology that was coming to the fore in biology. The second half of this chapter turns to Hugo de Vries, in which I clear up some of the many misconceptions that surround his work, how he adopted experimentalism, and elaborate upon the crucial theory that emerged from practice: that of the opposed variational types of fluctuations and mutations, which laid the basis for experimental evolution's central dispute covered in Chapters 4 and 5. Thus in the juxtaposition of Weldon and de Vries is further revealed the interplay of theory and

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<sup>178</sup> This chapter could also have included Wilhelm Johannsen as a key experimental evolutionist, but his work and theories were extensively picked up by and elaborated upon by the figures I focus on in Chapters 4 and 5, and thus would be redundant, and his published work did not include the ideological bent and methodological agitation that Weldon and de Vries emphasized. For some discussion of practical influences upon Johannsen, see Jean Gayon and Doris T. Zallen, "The Role of the Vilmorin Company in the Promotion and Diffusion of the Experimental Science of Heredity in France, 1840–1920," *Journal of the History of Biology* 31, no. 2 (1998): 241–262.

practice, with the underlying drive being that of practice. Although curiously in their work the notions of control and utility were entirely absent in Weldon's work and muted in de Vries'. (This was not the case for the latter's public remarks, an extensive discussion of which appears in the following chapter.) What united them however was that their vision was centered upon making evolution visible.

### **Making Evolution Visible by Statistics: Raphael Weldon**

Roughly a decade after the premature conclusion of Dallinger's experiment, Walter Frank Raphael Weldon began to study and make visible the *action* of natural selection in a more methodical fashion than anyone before him.<sup>179</sup> Upon reading Francis Galton's *Natural Inheritance* (1889), a statistical analysis of human inheritance, Weldon sought to further integrate statistics into the biological sciences, particularly to support Darwinism. The methods and philosophy that Weldon developed, alongside his statistician collaborator Karl Pearson, became known as biometry.<sup>180</sup> Weldon's goal was not to create an experimental evolution; instead, by graphing fine measurements of large samples, biometry would render the minutiae of biological variation, diversity, and evolution *visible*. While Darwin had studied artificial selection as "an experiment on a gigantic scale," Weldon was interested in wild populations of animals. In fact, Weldon's 1898 presidential address to the Zoological Section of the British Association for the Advancement of Science was considered by some, for decades, one of the few demonstrations of natural selection in action (and, critically, of directional selection).<sup>181</sup> Ironically, while Weldon, and the positivism of the biometrical program, intended to avoid causal claims in favor of descriptive correlations, his large-scale experimentation

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<sup>179</sup> Much of my analysis of biometry was influenced by Jean Gayon, *Darwinism's Struggle for Survival: Heredity and the Hypothesis of Selection* (Cambridge: Cambridge University Press, 2007). A reinterpretation of Weldon's career and thought is likely coming, due to Gregory Radick's forthcoming *Disputed Inheritance: The Battle over Mendel and the Future of Biology* (University of Chicago Press).

<sup>180</sup> Because he was the biologist of the pair, I focus on Weldon. Additionally, Weldon started down this path before becoming into contact with Pearson and it was Weldon who influenced Pearson to take up biological problems. For a discussion of Weldon's influence on Pearson's statistical methods, see M. Eileen Magnello, "Karl Pearson's Gresham Lectures: W. F. R. Weldon, Speciation and the Origins of Pearsonian Statistics," *The British Journal for the History of Science* 29, no. 1 (1996): 43–63. Magnello's article provides more detail on statistical methods, such as curve fitting, than I do here.

<sup>181</sup> The other example, Bumpus' study of sparrows, I mention in the following chapter. Jean Gayon, *Darwinism's Struggle for Survival: Heredity and the Hypothesis of Natural Selection* (Cambridge University Press, 1998), 197.

on Plymouth Sound crabs showed that understanding evolution *required* understanding causes through experimentation.

While Galton had done much to introduce statistics into several sciences, including meteorology and biological inheritance, Weldon brought the new science to bear on natural evolution. Weldon wrote in 1894, apparently disregarding Darwin's reliance on breeding,

The questions raised by the Darwinian hypothesis are purely statistical, and the statistical method is the only one at present obvious by which the hypothesis can be experimentally checked.<sup>182</sup>

The method was simple in theory, being “all questions of arithmetic”: calculate the “degrees of abnormality” between individuals and among organs, and their associated death rates. Then,

when we know the numerical answers to these questions for a number of species we shall know the direction and the rate of change in these species at the present day—a knowledge which is the only legitimate basis for speculations as to their past history and future fate.<sup>183</sup>

The biometricians were addressing the theoretical and methodological problem inherited from Darwin: gradualism. Galton, wrote in *Biometrika*, the new journal co-edited by Weldon and Pearson, that “the primary object of Biometry is to afford material that shall be exact enough for the discovery of incipient changes in evolution which are too small to be otherwise apparent.” He continued,

The organic world as a whole is a perpetual flux of changing types. It is the business of Biometry to catch partial and momentary glimpses of it, whether in a living or in a fossil condition, and to record what it sees in an enduring manner.<sup>184</sup>

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<sup>182</sup> Weldon, “Remarks on Variation in Animals and Plants. To Accompany the First Report of the Committee for Conducting Statistical Inquiries into the Measurable Characteristics of Plants and Animals,” *Proceedings of the Royal Society of London* 57 (January 1, 1894): 381. Pearson later wrote, Weldon's research “first formulated the view that the method of the Registrar-General [statistics] is the method by which the fundamental problems of natural selection must be attacked.” Karl Pearson, “Walter Frank Raphael Weldon. 1860-1906,” *Biometrika* 5, no. 1/2 (1906), 19.

<sup>183</sup> Weldon, “On Certain Correlated Variations in *Carcinus maenas*,” *Proceedings of the Royal Society of London* 54 (1893): 329.

<sup>184</sup> Francis Galton, “Biometry,” *Biometrika* 1, no. 1 (1901): 9–10.



The exact statistical study of evolution in wild populations would *make natural selection visible quantitatively*. Through rigorous statistical analysis and graphing trait variation and population mortality, biologists, they argued, could see what natural selection saw, while avoiding the artifice of laboratory work. Galton wrote, “biology could soon be raised to the status of a more exact science than it can as yet claim to be.”<sup>185</sup>

Thus, Pearson introduced *Biometrika* by arguing that “the evolutionist has to become in the widest sense of the words a registrar-general for all forms of life.” That is, a statistician. As was common in these days, Pearson pointed to Darwin as their predecessor: while Darwin may have applied rudimentary statistical thinking to his research, particularly in *Orchids*, Darwin’s letters revealed a naturalist who wished he knew more. Pearson compared the biometrization of Darwinism to Maxwell’s mathematization of Faraday’s electromagnetism.<sup>186</sup>

An advantage of the program, according to the biometricians, was that this method neither posited physiological causes nor rested upon direct experimentation. In a period mired by metaphysical speculations regarding the qualities and material causes of heredity and variation, the biometricians desired to simply describe and measure changes numerically.<sup>187</sup> For example, whether variation was continuous or discontinuous, would be masked by the “mathematics of large numbers.” (The work also moved beyond traditional Darwinian naturalism which naively explained *apparently* useful traits as selective adaptations.<sup>188</sup>) For Pearson, experimentation was a legitimate method, but:

When he [the evolutionist] cannot observe and measure in Nature, then he must experiment on “populations” within the laboratory. But few biological laboratories have

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<sup>185</sup> Galton, 10.

<sup>186</sup> Pearson, “Editorial: The Spirit of Biometrika,” *Biometrika* 1, no. 1 (1901): 4–5, 3.

<sup>187</sup> This also followed from Pearson’s philosophical idealism; see Theodore M. Porter, *Karl Pearson: The Scientific Life in a Statistical Age* (Princeton: Princeton University Press, 2004), 6–8. Note that Pearson’s philosophy of science is directly opposed by Bukharin’s philosophy of science of dialectical materialism.

<sup>188</sup> Gayon, *Darwinism’s Struggle for Survival: Heredity and the Hypothesis of Selection*, 214–16. As Bumpus soon noted in his statistically cruder and anti-Darwinian study, “We are so in the habit of referring carelessly to the process of natural selection, and of invoking its aid whenever some pet theory seems a little feeble, that we forget we are really using a hypothesis that still remains unproved, and that specific examples of the destruction of animals of known physical disability are very infrequent.” Hermon C. Bumpus, “The Elimination of the Unfit as Illustrated by the Introduced Sparrow, *Passer domesticus*,” in *Biological Lectures from the Marine Biological Laboratory at Wood’s Holl, Mass. 1898* (Boston, Mass.: Ginn & Company, 1899), 209–26.

the space or the resources needed for dealing with the vital changes of populations.<sup>189</sup>

Therefore, the biometrists considered statistics as not only the proper method by which to study evolution, but also the only available method.<sup>190</sup> It also avoided the problematic leap from the artificial to the natural: whereas Dallinger studied microbes living in a machine, the biometricians studied variation, inheritance, and selection among animal populations *in nature*. This position opposed the program of the contemporarily emerging experimental biologists, such as that of Wilhelm Roux's *Entwicklungsmechanik*, (and soon, the Mendelians) and was key to their coming conflict.<sup>191</sup>

*Biometrika* promulgated a program that Weldon had already worked out and conducted. He claimed in his first biometrical studies to have provided evidence of natural selection in action without resorting to causal claims (although this would change in 1898, discussed below). By measuring trait variations, he found that three different populations of shrimp (*Cragnon vulgaris*), while obeying the “law of error” (a normal bell curve), showed distinct differences., stability (he speculated) arising from stabilizing selection.<sup>192</sup> In additional work, he discovered that some correlation coefficients remained constant between races even if their means and curves differed.<sup>193</sup> Examining shore crabs (*Carcinus maenas*), Weldon found an asymmetrical distribution in frontal

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<sup>189</sup> “Editorial,” 3. Here he advocated for a “well-equipped Biometric Farm Laboratory, where breeding and survival experiments on large numbers could be carried out with ample room and care and, when necessary, for long periods.” I discuss the proposals for such farms and laboratories in the following chapter.

<sup>190</sup> Charles H. Pence, ““Describing Our Whole Experience”: The Statistical Philosophies of WFR Weldon and Karl Pearson,” *Studies in the History and Philosophy of Biological and Biomedical Sciences* 42, no. 4 (2011): 475–485. Pence usefully distinguishes between the statistical philosophies of Weldon and Pearson despite their shared methods. Pearson held to a stricter positivism that used statistics to reduce various phenomena to mathematical relationships, whereas Weldon embraced statistics as a way to capture the considerable variation of the world while avoiding unjustified physiological speculation. As Pence writes, biological complexity meant that “correlation is the only type of connection that can be drawn between biological systems of the kind Weldon was interested in investigating...” (p. 482). The initial avoidance of experimentation was therefore due to more practical concerns.

<sup>191</sup> See Jane Maienschein, “The Origins of *Entwicklungsmechanik*,” in *Developmental Biology: A Comprehensive Synthesis*, vol. 7, ed. Scott F. Gilbert (New York: Plenum Press, 1991): 43–62.

<sup>192</sup> Already, Weldon was beginning to posit causes, pointing to the limitations of the program: He suggested that the separate curves he detected were not due to heredity as Galton might hold, but instead was due to the “selective action of the surrounding conditions – an action which must vary in intensity in different places.” Weldon, “The Variations Occurring in Certain Decapod Crustacea. I. *Cragnon Vulgaris*,” *Proceedings of the Royal Society of London* 47 (1889): 451. Gayon notes that this stance contradicted Galton’s theory as well. Gayon, *Darwinism’s Struggle for Survival*, 203.

<sup>193</sup> This led him to wonder if these correlations explained taxonomic differences. Weldon, “Certain Correlated Variations in *Cragnon Vulgaris*,” *Proceedings of the Royal Society of London* 51 (1892): 11.

breadth (measured “from tip to tip of the anterior lateral teeth”) in the sample from Naples. He consulted Pearson, marking the beginning of their collaboration, who demonstrated that the curve could be composed of two different morphs with disparate means and probable errors, i.e., the females exhibited dimorphism. Gayon suggests that Weldon considered this a possible snapshot of evolution in action, Darwin’s “divergence of character,” but he decided not to follow this population through its generations.<sup>194</sup>

In the meantime, a group of scientists — Weldon, Galton, Francis Darwin, and E. B. Poulton, among others — established a Committee for Conducting Statistical Inquiries into the Measurable Characteristics of Plants and Animals, later referred to as the Evolution Committee.<sup>195</sup> While this organization published several significant reports — particularly, Weldon’s, and later, William Bateson’s and Edith Saunders’ first reports on genetics — it had a rocky and mostly unproductive history.<sup>196</sup> The Evolution Committee’s first major project was an attempt to replicate in herring the detection of dimorphism, but despite the accumulation of good data, the Committee’s practical failure to resolve that data statistically prevented Weldon from publishing.<sup>197</sup> The Committee’s study of ox-eye daisies also failed. Weldon conducted laboratory “experiments on repeated selection of infusoria,” but again, never published the work.<sup>198</sup>

Weldon changed his strategy, hoping to discover “selective destruction,” or a death-rate due to natural selection, occurring in a wild population, and in so doing unveiled a new way to study evolution in action.<sup>199</sup> Published as a report to the Evolution Committee, Weldon sought to convince the biological community of his method’s power.

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<sup>194</sup> With only this study, the dimorphism could be explained by Galtonian selection-by-replacement or by Darwinian selection-by-disruption. Gayon, *Darwinism’s Struggle for Survival*, 209–10. This distinction, as emphasized by Gayon and Stoltzfus & Cable, would be critical for later theories of evolution following the rediscovery of Mendel.

<sup>195</sup> It was initially proposed as the Committee for the Statistical Enquiry into the Variability of Organisms. In 1897, it expanded its scope to “accurate investigation of Variation, Heredity, Selection, and other phenomena relating to Evolution.” Pearson, “Walter Frank Raphael Weldon. 1860-1906,” 23.

<sup>196</sup> William B. Provine, *The Origins of Theoretical Population Genetics* (Chicago: University of Chicago Press, 1971), 48–51, 54–55.

<sup>197</sup> Gayon, *Darwinism’s Struggle for Survival*, 211; Magnello, “Karl Pearson’s Gresham Lectures,” 59–61.

<sup>198</sup> Pearson, “Walter Frank Raphael Weldon. 1860-1906,” 24, 22.

<sup>199</sup> Weldon, “Report of the Committee, Consisting of Mr. Galton (Chairman), Mr. F. Darwin, Professor Macalister, Professor Meldola, Professor Poulton, and Professor Weldon, ‘for Conducting Statistical Inquiries into the Measurable Characteristics of Plants and Animals.’ Part I. ‘An Attempt to Measure the Death-Rate Due to the Selective Destruction of *Carcinus moenas* with Respect to a Particular Dimension,’” *Proceedings of the Royal Society of London* 57 (1894): 360-379.

For this study, Weldon measured several dimensions among 7,000 adult female crabs in Plymouth Sound (again, *Carcinus maenas*, but a different population) that swarmed the beach below the Marine Biological Station at which he worked: the carapace length (to standardize growth), frontal breadth, and “right dentary margin” (distance between the end teeth of one side).<sup>200</sup>

With the data, Weldon developed statistical formulas to calculate and graphically depict selective destruction. He estimated that 7.7% of the population was eliminated due to differences in frontal breadth. In contrast, natural selection was *not* acting upon the “right dentary margin” because variation in length increased with growth.<sup>201</sup> While he did not consider the exact numbers reliable, “the point which seems worthy of confidence” and possibly of “very great importance, is the *form* of the result.”<sup>202</sup> “By pure statistical methods, and without making any [physiological] assumptions,” he had determined “the time of life which natural selection must be assumed to act, if it acts at all” *and* a “numerical estimate” of selective destruction as a function of frontal breadth. In essence he had detected natural selection at work.<sup>203</sup>

But while Weldon had shown how to “determine the direction and rate of evolution,” he was dissatisfied by the lack of explanation: why was a wider frontal breadth disadvantageous? To understand its “physiological function” and “functional adaptation,” he was forced to experiment. Working under a barrage of criticisms, Weldon expanded the study into large-scale experimentation.<sup>204</sup> Five years later, he reported — as

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<sup>200</sup> Weldon, “Opening Address of the Zoological Section,” *Nature* 58, no. 1508 (1898): 504.

<sup>201</sup> Weldon, “An Attempt to Measure the Death-Rate Due to the Selective Destruction of *Carcinus moenas*,” 368. Weldon interpreted the relationship between variation and growth as consistent with “Darwin’s statement that many variations appear at a late period of development.” He noted, however, that without experiment, it was possible but unlikely that the plateauing and shrinking of frontal breadth was merely a condition of growth in crabs.

<sup>202</sup> *Ibid.*, 371. Emphasis mine. The power of this method was its possible generality, although it had several limitations. It would fail if directional selection were too strong, as in “rapid changes such as those induced artificially by domestication,” which was outside of his concern, or if there was rapid migration or changes in the environment. The method also covered only traits with a normal distribution, but Weldon considered violations to be the exception: only one crab in 5,000 had a “right dentary margin” outside the probable error.

<sup>203</sup> Pearson was critical of Weldon’s claim to have causally linked frontal breadth and natural selection. Charles H. Pence, “‘Describing Our Whole Experience’: The Statistical Philosophies of WFR Weldon and Karl Pearson,” *Studies in the History and Philosophy of Biological and Biomedical Sciences* 42, no. 4 (2011/12): 475-485.

<sup>204</sup> Pearson complained about the vitriol the 1894 publication engendered, despite his caution and admission of limitations. Pearson, “Walter Frank Raphael Weldon. 1860-1906,” 26.

President of the British Association's Zoological Section — a further study of *Carcinus maenas*, in which he had experimentally determined the frequency and *cause* of the death-rate due to variation in frontal breadth.<sup>205</sup>

In fact, “the mean frontal breadth of this race of crabs is, in fact, changing at a rate sufficiently rapid for all the requirements of a theory of evolution.”<sup>206</sup> Statistical data had revealed that between 1893 and 1898, the frontal breadth of both male and female *Carcinus maenas* had measurably *decreased*. He could therefore also counter the claim that Darwinism relied on an unimaginable amount of “fortuitous variation” that was too minute for selection to detect: it simply did.

The sophisticated and large-scale experimentation he conducted also left him “confident” as to the causal link between selection and frontal breadth: environmental changes in Plymouth Sound. Over the previous half-century, Plymouth Sound had become blocked by a “huge artificial breakwater” that had curbed water flow. A number of rivers deposited china clay into the water, but instead of being washed out to sea, the clay now settled and accumulated. As the surrounding human population grew, an increasing amount of sewage and garbage was thrown into the water. These changes had noticeably eliminated several animals from occupying the space (while they continued to inhabit the area on the other side of the breakwater). For Weldon, the situation created an obvious selective condition to explain decreasing frontal breadths of *Carcinus maenas*.

Weldon constructed a “large vessel of sea-water, in which a considerable quantity of very fine china clay was suspended ... by a slowly moving automatic agitator.” Raising 248 crabs, he measured the frontal breadths of the 154 that died and the 94 that survived. The mean of the surviving sample was smaller than that of the original population and the mean of the dead sample larger. When he used coarser clay, this difference was smaller and “not selective.”<sup>207</sup> Weldon, believing he had sufficiently replicated natural conditions within this artificial environment, argued,

I see no shadow of reasoning for refusing to believe that the action of the mud upon the beach is the same as that in an experimental aquarium; and if we believe this, I see no

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<sup>205</sup> Weldon, “Opening Address of the Zoological Section.” Weldon framed his address as a defense of Darwinism, arguing that his methods showed that selection had the available variation to act upon despite its minuteness.

<sup>206</sup> Weldon, 504.

<sup>207</sup> Weldon, 505.

escape from the conclusion that we have here a case of Natural Selection acting with great rapidity with which the conditions of life are changing.<sup>208</sup>

Before confirming this conclusion, Weldon performed a control experiment. If selection were truly acting on this trait, then “protecting” the broader crabs from suspended clay should produce an adult population in which the mean did not diminish. To do this, Weldon “established an apparatus consisting of *some hundreds* of numbered glass bottles, each bottle being provided with a constant supply of clean sea-water by means of a system of glass syphons. Into each of these bottles [he] placed a crab from the beach.”<sup>209</sup> (See Figure 2.)



Figure 2. From Karl Pearson, “Walter Frank Raphael Weldon. 1860-1906” (1906), Plate IV. Weldon’s “experimental crabbery.”

<sup>208</sup> Weldon, 505.

<sup>209</sup> Weldon, 506. Emphasis mine.

Pearson was astonished by the project, writing that “the labour involved was excessive”:

One "crabbery" consisted of 500 wide-mouthed bottles ... and each crab had to be fed daily and its bottle cleaned. During the summer of 1897 Weldon spent the whole of his days at the aquarium, and his wife hardly left him except to fetch the needful chop.<sup>210</sup>  
The sewage experiment was "horrible from the great quantity of decaying matter necessary to kill a healthy crab."<sup>211</sup>

Following each of an individuals' molts, Weldon measured the length and frontal breadth of the crab's shell, finding that when compared to a wild crab of the same length, the difference was “a little less.”<sup>212</sup> He explained this by attributing selective action upon acclimatization. Acknowledging the difficulty of keeping the apparatus clean, he performed *another* control experiment in which the crabs were raised in “putrid water” and those that survived again had “distinctly” smaller frontal breadths than the dead. But under clean conditions, the adult crabs were “unmistakably *broader* than wild crabs of their own size.”<sup>213</sup>

Weldon remained cautious. He acknowledged that his assumption that size and age were directly correspondent had not been demonstrated and that the bottles, an artificial environment, could unintentionally impact growth. Indeed, “we could not accept this experiment by itself as proof that some selective agent exists on the shore which is absent from the bottles.” But, the experimental results were “in complete harmony” with the hypothesis that the increase in suspended mud was “the selective agent” making crabs in Plymouth Sound narrower. Further, contrary to his conclusion five years prior, Weldon posited a physiological explanation: dead crabs had gills covered with china clay and survivors did not, i.e., “narrow frontal breadth [probably] renders one part of the process

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<sup>210</sup> Pearson noted earlier in his obituary that Weldon's wife Florence computed data alongside him.

<sup>211</sup> Pearson, “Walter Frank Raphael Weldon. 1860-1906,” 27. Pearson does not cite this quotation, but I presume that it comes from a letter to Pearson from Weldon.

<sup>212</sup> Weldon, “Opening Address of the Zoological Section,” 506. Gayon points out that Weldon explicitly relied upon the developmentalist views of Darwin and Weismann; this would conflict with the genotype-phenotype distinction followed by the geneticists.

<sup>213</sup> Weldon, 506.

of filtration more efficient than it is in crabs of greater frontal breadth.”<sup>214</sup>

Thus, Weldon concluded, that in addition to the utility of statistics in describing variation,

I hope I have convinced you that the action of natural selection upon such fortuitous variations can be experimentally measured, at least in the only case in which any one has attempted to measure it. I hope I have convinced you that the process of evolution is sometimes so rapid that it can be observed in the space of a very few years. ... Numerical knowledge of this kind is the only ultimate test of the theory of Natural Selection...<sup>215</sup>

Weldon had produced a rich combination of experimentation, statistics, and field naturalism. By the end, Weldon’s work did not demonstrate Pearson’s anti-materialist and idealist philosophy, but it was still shot through with his pioneering statistical methods that was born from it.<sup>216</sup> Rather than deploying statistics to avoid causal reasoning, Weldon pointed to a plausible environmental mechanism that explained evolutionary change in a methodical and controlled manner. Moreover, he claimed that evolution had been observed in action.

However, the apparent success of the experimentation left Weldon underwhelmed by his overall project. Gayon writes, “It was because this purely ‘statistical’ approach was mathematically and materially too complex that Weldon turned to a classical experimental method, with all that implied in terms of causal hypotheses and laboratory procedures.” He further points out that the biometrical emphasis on sticking to correlations between parent and offspring had not been calculated at all in the work and the precise physiological explanation about gills remained speculative.<sup>217</sup> Weldon had shown the immense amount of rigor required to study evolution and selection in nature, and that it was possible.

Like Dallinger and despite his apparent success, Weldon’s evolutionary

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<sup>214</sup> Weldon, 506.

<sup>215</sup> Weldon, 506.

<sup>216</sup> This is consistent with Pence regarding Pearson and Weldon in “Describing Our Whole Experience.”

<sup>217</sup> Gayon, *Darwinism’s Struggle for Survival*, 223. Gayon also accepts the argument that Pearson’s phenomenology undermined their project: “The major epistemological weakness of the biometricians lay in their intransigent phenomenalist epistemology. Fueled by their enthusiasm, this method led them to believe that the theory of natural selection could be constructed without any biological hypotheses whatsoever...” (Gayon, 251).



experimentation did not launch a research program.<sup>218</sup> But this was not because he abandoned experimental evolution. Even with his growing emphasis on biometry via his editorship of *Biometrika*, Pearson considered Weldon “essentially a field naturalist.” According to Pearson, Weldon was “impelled” to biometry because he thought “no further progress with Darwinism could be made until demonstration from the statistical side was forthcoming.” Weldon’s image as a statistician, rather than an experimentalist, likely originated not only from his criticism of experimental genetics, but because he failed to publish much of his work, whether experimental or field-based. In addition to the experiments on infusoria, he also worked with *Daphnia*, “which had shown him how widely *Daphnia* are modified by their chemical and physical environment, and how this modification is largely due to selection.”<sup>219</sup> He also studied the caterpillars of pedigree moths, “his first big experimental investigation into heredity,” lasting three years. (Unfortunately for Weldon, “no definite inheritance at all of the character selected for consideration was considered.”) Weldon’s published work on snails hoped to “get to the kernel of selection in its action on local races,” but unlike the crab work, no experimentation was involved.<sup>220</sup> Thus, Weldon, like Dallinger, pointed to the possibilities of experimental evolution, but did not develop a lasting program for others to help conduct. Had he succeeded to publish more of his work, it is possible his experimental research would have been equally as famous as the statistical. But Weldon’s unfortunate and early death in 1906 at the age of 46 prevented that from ever occurring. Despite his feud with geneticist William Bateson, Weldon’s demonstration and elaboration of *statistical methods* impacted the American experimental evolutionists who fruitfully integrated the feuding programs mostly along Mendelian lines (Chapters 4 and 5).

### Bateson's Critique of the Biometrical Method

Essential to this story, however, is the acrimonious debate between Weldon and geneticist William Bateson. Here, I focus specifically on Bateson’s searing

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<sup>218</sup> Note that Weldon’s research, too, was published as an address, not a research article or monograph.

<sup>219</sup> Pearson, “Walter Frank Raphael Weldon. 1860-1906,” 31.

<sup>220</sup> Pearson, 32.

methodological critique of biometry, for it demonstrates the growing need for experimentation that many biologists perceived at the time (setting aside the theoretical debate over the law of ancestral inheritance). From this exchange, I suggest that biometry — as the biometrists envisioned it — failed partially because of its programmatic neglect of experimentation, broadly construed. While their statistical methods were embraced by geneticists after Bateson, the *program* as envisioned by Pearson and Weldon was insufficient. That is, biometry appeared to make evolution *visible*, but it glossed over hereditary and evolutionary complexities to such a degree that biometry *alone* did not throw light on much at all, especially when it came to questions of control.

Bateson's critique of biometry, and much of evolutionary science in general, was that its fundamental method was hopelessly flawed.<sup>221</sup> Biometrists treated "the indiscriminate confounding of all divergences from type into one heterogeneous heap under the name "Variation" which "creat[ed] an enduring obstacle to the progress of evolutionary science."<sup>222</sup> According to Bateson, the biometrists' methods were contrary to Darwin's, in that they treated

the evidence of the collector, the horticulturist, the breeder, the fancier ... with neglect, sometimes, ... with contempt. That wide field whence Darwin drew his wonderful store of facts has been some forty years untouched. ... For the concrete in evolution we are offered the abstract.<sup>223</sup>

Instead, Bateson was "convinced that the investigation of heredity by experimental methods offer[ed] the sole chance of progress with the fundamental problems of

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<sup>221</sup> In this address, Bateson called biometrists "Ancestrians," referencing their promotion of the law of ancestral inheritance. It was this adherence that many geneticists attacked as incongruent with biology, which they alleged undermined Pearson's positivist program. Again, however, I am here interested in methods, not theories.

<sup>222</sup> William Bateson, "Opening Address of the Zoological Section," *Nature* 70 (August 25, 1904): 407. He specifically pointed out the "heterogeneous" characters of variation as "quantitative or qualitative, permanent or transitory, in size, number of parts, chemistry, and the rest." Ironically, though, Karl Pearson had criticized Bateson in 1902 for sloppy, incoherent, and inconsistent definitions of "variation" and "discontinuity." Karl Pearson, "On the Fundamental Conceptions of Biology," *Biometrika* 1, no. 3 (1902): 320–44. Pearson further criticized Bateson for never testing the inheritability of "discontinuous variations" and developing a method by which to distinguish such variations from "continuous" or "normal" variation. This highlights how essential Mendel and Johannsen were: Bateson could not have undermined biometry without them.

<sup>223</sup> Bateson, "Opening Address of the Zoological Section," 407.

evolution.”<sup>224</sup> Furthermore, like Darwin (and Mendel), he embraced the artificial: “The breeding-pen is to us what the test-tube is to the chemist.”<sup>225</sup> Bateson’s rhetoric adopted Darwin’s metonymy regarding the natural and artificial:

In the natural world, in the collecting-box, the seed-bed, the poultry-yard, the places where variation, heredity, selection may be seen in operation and their properties tested, answers to these questions meet us at every turn—*fragmentary answers*, it is true, but each direct to the point. ... If he [anyone] breed two or three generations of almost any controllable form, he will obtain immediately facts as to the course of heredity which obviate the need for much laborious imagining.<sup>226</sup>

Bateson also believed genetics “will be found of extraordinary use.”<sup>227</sup> While the phylogenetic studies he had pursued perhaps revealed “the history ... of Evolution,” genetics “deal[t] not only with the present and the past, but with the future also.”<sup>228</sup> He quoted Francis Bacon,

I entreat men to believe that it is not an opinion to be held, but a work to be done; and to be well assured that I am labouring to lay the foundation, not of any sect or doctrine, but of human utility and power.<sup>229</sup>

Bateson also argued that the biometric theory discouraged experimentation. He reiterated this critique more forcefully in 1909:

By suggesting that the steps through which an adaptive mechanism arose were indefinite and insensible, all further trouble is spared. While it could be said that species arise by an insensible and imperceptible process of variation, there was clearly no use in tiring ourselves by trying to perceive that process. This labour-saving counsel found great favour.<sup>230</sup>

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<sup>224</sup> Bateson, 409.

<sup>225</sup> Bateson, 409. In his 1902 defense of Mendel, he wrote “the breeder ... will be second only to the chemist in resource and in foresight.” William Bateson, *Mendel’s Principles of Heredity: A Defence, with a Translation of Mendel’s Original Papers on Hybridisation* (Cambridge: Cambridge University Press, 1902), 208.

<sup>226</sup> Bateson, “Opening Address of the Zoological Section,” 407. Emphasis mine.

<sup>227</sup> Bateson, 413. Olby points to the irony that Bateson’s “objections to utility were deep,” yet “Bateson did much more for horticulture, and indirectly, for agriculture, (through Biffen) than possibly any other British biologist of his generation.” Robert Olby, “The Dimensions of Scientific Controversy: The Biometric-Mendelian Debate,” *The British Journal for the History of Science* 22, no. 3 (1989): 318.

<sup>228</sup> Bateson, “Opening Address of the Zoological Section,” 409.

<sup>229</sup> Bateson, 409. Bacon’s quote comes from *Great Instauration*.

<sup>230</sup> William Bateson, “Heredity and Variation in Modern Lights,” in *Darwinism and Modern Science*, ed. A. C. Seward (Cambridge: Cambridge University Press, 1909), 99.

To summarize, Bateson regarded biometry and traditional Darwinian studies to be following the *wrong* method. It was genetics, not biometry, that rendered evolution *visible, controllable, and useful*. Bateson argued that while the biometricians may have adopted Darwin's theory of natural selection, it was the Mendelians who had adopted Darwin's *method* — experimentally and rhetorically. The argument here, therefore, is that during “the eclipse of Darwinism,” it is crucial to distinguish between Darwinian theory and Darwinian method. Darwin did not develop his theory of evolution by natural selection by studying animals in the wild via statistics, but by engaging in hands-on experimentation (even if not a long-term selection experiment), by considering physiological mechanisms, and by embracing the artificial world of the breeders. In this sense, the Mendelian adoption of Darwinian method reshaped Darwinian theory.<sup>231</sup>

### **Making Evolution Visible by Experiment: Hugo de Vries**

Contemporary with Weldon, the Dutch botanist Hugo de Vries developed another scientific program, culminating in his landmark publication of 1900, *Die Mutationstheorie*, which expounded fifteen years of work on experimental evolution.<sup>232</sup> While known primarily for its lengthy observations on the evening primrose, *Oenothera lamarckiana*, its legacy was far more substantial. It promulgated an experimental ideology that was still just emerging within the evolutionary sciences, proposed theories that would fuel twenty years of debate, and bolstered the Darwinian legacy by integrating natural history with agriculture and horticulture.

Hugo de Vries remains an enigma, however, presenting a number of paradoxes in the historical literature.<sup>233</sup> While he considered himself a follower of Darwin, he is known as an anti-Darwinian. He was one of the co-discoverers of Mendel, yet rejected its fundamentality. Christened the “godfather of experimental evolution” by Charles

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<sup>231</sup> Arlin Stoltzfus and Kele Cable, “Mendelism-Mutationism: The Forgotten Evolutionary Synthesis,” *Journal of the History of Biology* 47, no. 4 (2014): 501–46.

<sup>232</sup> Hugo de Vries, *The Mutation Theory: Experiments and Observations on the Origin of Species in the Vegetable Kingdom*, vol. 1, trans. John Farmer and Arthur Darbishire (Chicago: Open Court Pub. Co., 1909).

<sup>233</sup> Bert Theunissen, “Knowledge Is Power: Hugo de Vries on Science, Heredity, and Social Progress,” *The British Journal for the History of Science* 27, no. 4 (1994): 291–311.

Davenport, his *Oenothera* work, usually the only science of his presented by historians, is remarkably non-interventionist. Furthermore, as the rest of the dissertation will demonstrate, much of the distortion and confusion regarding both de Vries as well as those whom he inspired (particularly Edward East and George Shull) results from not seriously interrogating what is meant by terms such as “mutation,” “fluctuation,” “selection,” and “species.” Because the meanings of these terms changed substantially between Darwin and the Modern Synthesis, they cannot be taken as rigid categories, but as contingent ideas specific to the individual historical scientists.<sup>234</sup> Thus reassessing de Vries’ position in the history of experimental evolution is important to understanding the history of experimental evolution in general.

The Mutation Theory was not based solely upon *Oenothera*, but on a number of additional pillars, including breeders’ and scientists’ experiences with horticulture and agriculture (although this was complicated), problems with the theory of natural selection, his experimental treatments of regression and nutrition, and to some extent, the rediscovery of Mendelism.<sup>235</sup> The experimental species were also not restricted to *Oenothera*, and included maize, poppies, chrysanthemums, coriander, and dill, among others. Thus, any simplistic description of de Vries’ mutation theory usually results in distortion, because to explain it requires explaining its ontological and epistemological basis.

De Vries’ method was a mixture of natural history, experimentation, and statistics. Despite the later disputes between biometry with Mendelism and mutationism, de Vries embraced biometry (although not with the same sophistication as Pearson), applying the statistical methods of Quetelet and Galton to his own plants and confirming that variability matched a predictable bell curve.

For de Vries, the mutation theory and experimental evolution were virtually identical, and opposed to gradualism. The naturalists’ rejection of experimental evolution “has its root ... in the opinion that the species of animals and plants have originated by imperceptible gradations,” “so slow that the life of a man is not long enough to enable

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<sup>234</sup> For an example, see Luis Campos’ discussion of geneticists’ changing use of “mutation” and “mutant” in the 1920s in *Radium and the Secret of Life*, 175-180.

<sup>235</sup> Arlin Stoltzfus and Kele Cable, “Mendelism-Mutationism: The Forgotten Evolutionary Synthesis,” *Journal of the History of Biology* 47, no. 4 (2014): 501–46.

him to witness the origin of a new form.” Instead, de Vries argued that “...species arise by saltations and that the individual saltations are occurrences which can be observed like any other physiological process.”<sup>236</sup> Thus, this combination of method and theory would not only render evolution *visible*, but also asserted that evolution *was* visible.

The visibility of evolution was the key result of de Vries’ *Oenothera* research, which were remarkably and ironically not all that experimental. Indeed, de Vries wrote that “the object of the experiments in my garden was not to induce mutations, but to make a closer study of the process of mutation than was possible in nature.” That is, his “experiments” were more like a closely tracked natural history of *Oenothera* under observable conditions. The point was *not* to “determin[e] the causes of these processes,” but to simply observe the process in the first place, under controlled, well-nourished conditions free from “the sources of error and uncertainty,” such as insect fertilization.<sup>237</sup> This was not all that different from Weldon.

De Vries also criticized the reckless use of breeders’ testimonies as scientific evidence. Although Darwin’s use of such had provided key support for the theories of selection and common descent, “the ‘doctrine of selection’ require[d] a new set of facts. Since Darwin, a new standard of evaluation of facts has come to be.”<sup>238</sup> He believed that experimentalism’s embrace of reductionism and simplicity to isolate patterns and laws conflicted with breeders’ need for complexity and hybridization (i.e., contamination) for commercial use. Breeding had questionable relevance to the origin of species; it could “not help us to choose” between the selection and mutation theories. De Vries argued that biologists should “fix our attention on the simplest processes,” with crossing excluded, so that the effects of mutation and selection could be revealed.<sup>239</sup> Until then, most historical and even experimental claims could not properly differentiate between the two factors of selection and mutation. De Vries did not reject agriculture and horticulture as important

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<sup>236</sup> Hugo de Vries, *The Mutation Theory*, viii.

<sup>237</sup> De Vries, 1909, pp. 300-301, 500-501. “The point is that the cultures in the garden disclose to us what happens, but ordinarily escapes observation, in nature.” p. 307 It was also important to determine how hybridization worked within the group. “The experiment does not create anything new. It merely enables us to see and study what happens in nature.”

<sup>238</sup> De Vries, 1909, pp. 12-13. In a way this was an extension of de Vries’ mentor Julius Sachs’ arguments regarding laboratory science versus Darwin’s amateur experimentation. Soraya de Chadarevian, “Laboratory-Science versus Country-House Experiments: The Controversy between Julius Sachs and Charles Darwin,” *The British Journal for the History of Science* 29 (1996): 17-41.

<sup>239</sup> De Vries, 1909, p. 82

sources of information, but emphasized the limitations.

As Theunissen suggests of Darwin, de Vries argued that the type of breeding a biologist paid attention to would color the evolutionary theory they expounded, a primary division being between agriculture and horticulture. In horticulture, new varieties appeared suddenly which were then “made constant by selection.” However, “it would be more correct to say that they are freed from the adulterating effects of free crossing.” That is, selection did not have “any object other than the purification of the new race from the effects of mixed ancestry.” (This claim was very important for his followers, discussed in Chapters 4 and 5.) Agriculturists, in contrast, gradually improved crops by selecting extant variation, but the race deteriorated once selection was relaxed. In neither case did selection have permanent and creative effects.<sup>240</sup> However, the method of agriculture, “which can only be achieved by a few and at the cost of great sagacity and patience, produces a great impression”; horticulture’s reliance on chance “makes none at all.” Therefore, agricultural methods “loomed much larger in our discussions on the origin of species.” But de Vries argued that horticulture bore stronger resemblance to evolution because it produced the constancy that the latter depended upon.<sup>241</sup>

De Vries held that the theory of selection, especially Wallace’s, who at this point was considered an ultra-selectionist by critics, rested upon two “unproved” hypotheses: that “the advance brought about by selection may increase for an indefinite period” and that “the result of selection can become independent of selection.” He worried that the first hypothesis, which usually entailed a belief that selection would take thousands of generations to effect creative change, “deterred many investigators from instituting experiments of this kind.” But, selection experiments that attempted to transform wild carrots, radishes, and parsnips into something akin to their cultivated form took only a few years. However, they reverted to their wild forms if selection slackened — regression — and therefore, despite their changes, the plants’ traits did not become “independent of selection.” Furthermore, even when selection continued, progress halted; therefore,

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<sup>240</sup> De Vries also points out that these two methods lead to different market effects. In horticulture, the sudden but permanent appearance of a novelty means the breeder has a monopoly only if they did not sell it. In agriculture, the need for rigid selection combined with its gradual improvements meant that it could be sold during the course of improvement and the breeder to some degree keeps their monopoly.

<sup>241</sup> Ibid., pp. 78-82

selection could not advance “for an indefinite period” and any recourse to eons of time were “absolutely without foundation.” Instead, selection “becomes gradually more difficult to effect any change until finally it becomes impossible.”<sup>242</sup>

The breeding work de Vries thought most fit for the job for examining selection was with sugar beets, of which breeders had doubled its sugar content by artificial selection. “All this has been done by selection of the best individuals afforded by ordinary fluctuating variation. Neither spontaneous variations nor crossings have played any part in it. We are dealing here with the process in its simplest form.” However, as impressive as these results were, they did not address the question of selection, evolution, and the origin of species. The sugar content in beets had doubled under artificial selection, but “by no manner of means is the improvement independent of selection.” Failure to keep up rigid selection on all target characters “would soon lead to a degeneration of the whole race.” The same was true of the cereals.<sup>243</sup>

From a series of experiments comparing and combining the effects of selection with nutrition, de Vries developed a crucial distinction between inherited and non-inherited variation that animated decades of debate, that between “fluctuations” and “mutations.” Instead of relying only on breeders’ work, de Vries began in 1891 to test the relative powers of selection and nutrition (manuring) to modify plants. In a four-way comparison between positive and negative selection and manuring and lack thereof with *Oenothera laevifolia* (a subspecies of *Lamarckiana*). De Vries found that over three generations, the positive effects of manuring overwhelmed negative selection. “Positive selection has, in combination” with nutrition, “only been able to achieve very little more.” In another condition, in which de Vries grew seedlings in pots instead of in the garden, “and without any selection at all, an exceptionally high nutrition had a far better result than the first two combinations.”<sup>244</sup> In further experiments, de Vries discovered the relative powers of each varied among the six species he tested. Thus, de Vries did not argue that selection

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<sup>242</sup> De Vries, 1909, pp. 85, 89, 119-120. De Vries suggested that Darwin’s view that introduction to cultivation engendered variability in plants was probably due to the existence of several subspecies within the initial population, as well as the increased population size.

<sup>243</sup> Ibid., p. 100, 104-106. De Vries also supported his theorization through selection experiments on maize conducted by Fritz Mueller and himself. Ibid., pp. 71-74

<sup>244</sup> Ibid., p. 537. De Vries ended the experiments after four generations because regression began to take hold.



was without effect, but that its effects were not straightforward either.<sup>245</sup>

Methodologically, de Vries concluded that biologists should keep nutrition as constant as possible, and “not to be too ready to interpret any changes that may occur as the effects of selection.”<sup>246</sup> His theoretical conclusions were more profound, however, and were the foundation of decades of debate over the relationships between variation, heredity, and selection, a debate that will be followed throughout the rest of the dissertation, for their implications in evolutionary theory as well as the possibility of taking control of evolution.

The central contradiction emanating from these experiments was *how evolution produced novelty*. For one, selection’s power was limited by regression and nutrition. It also eliminated variation. Another problem was that specific characters, those that differentiated species from each other, “are absolutely independent of selection.” However, most agricultural varieties, the evidence that much of the selection theory rested upon, did not have traits independent of selection. Indeed, it was “the instability of races” that served as “the central fact on which all agricultural breeding processes are based.”<sup>247</sup> Selection and agriculture thus went hand-in-hand, but they said little about the origin of species.

Quoting philosopher Paul Janet, who stated that “the real difficulty of Darwin’s theory is the transition from artificial to natural selection,” de Vries wrote:

This difficulty can only be surmounted by admitting that the improvement of races and the origin of new forms are really entirely different, and only apparently similar, processes. In Darwin’s time no distinction was drawn between these two processes.<sup>248</sup>

Thus, the core claim of de Vries’ mutation theory was that there were essential differences between the natural and artificial (although this specific claim was not necessarily adopted by his followers). Returning to the distinction between agriculture

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<sup>245</sup> Ibid., p. 573. One especially interesting case was that of Chrysanthemum, which sown from packets of mixed seeds showed a dimorphic curve (as Weldon saw in crabs). Assuming this to be the result of two races, a round of negative selection then produced a monomorphic curve. That is, selection reduced variation within a mixed population (pp. 562-565).

<sup>246</sup> Ibid., p. 543.

<sup>247</sup> Ibid., pp. 90-91, p. 129.

<sup>248</sup> Ibid., p. 211. These remarks are especially interesting given the arguments of Abeles regarding Darwin’s rhetoric of metonymy. It appears that de Vries recognized it as such, although not explicitly.

and horticulture, in which the associated dominant factors of evolution were selection and mutation, respectively, de Vries singled out mutation as the creative factor of evolution. More than that, de Vries in some sense constructed two parallel processes of variation-heredity-selection modeled on the distinction between agriculture and horticulture. The key was that there were two kinds of variation with physiological and evolutionary differences: fluctuations and mutations.

De Vries argued that his distinction between fluctuations and mutations was rooted in Darwin's original theory, but critiqued Darwin for his "lack of definiteness." That is, "Darwin was never quite clear about the physiological part of the theory of Selection." Instead, he see-sawed between emphasizing "single variations" (i.e., sports) or "individual variation" (i.e., small, ever-present, multi-directional). Much of the mission of *Die Mutationstheorie* then, was to not only experimentalize evolution, but to physiologically distinguish between kinds of variation. De Vries rechristened Darwin's "single variation" and "individual variation" as "mutation" and "fluctuation," respectively.<sup>249</sup> But he also theorized that fluctuations were inherited only partially and temporarily, whereas mutations were inherited fully and permanently.

De Vries' experiments on selection and nutrition were therefore a study of fluctuations. He generalized that fluctuating variability resulted from some combination of "selection, i.e., by the characters of its parents and grandparents and partly by nutrition, i.e., by the operation of external influences on the individual itself." But because the ancestors themselves "were also determined by the conditions of life," this variation was the result entirely of external conditions. Fluctuating variability, subject to statistical laws, was "the physiology of nutrition." but the "external causes of mutation are, on the other hand, as yet wholly unknown."<sup>250</sup>

Therefore, "mutation and the actual process of mutating must become the object of investigation." The problem was that catching mutations in the act of happening had been

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<sup>249</sup> De Vries, 1909, pp. 5, 29. A reason de Vries considered himself a part of the Darwinian heritage is that he argued Darwin himself relied on single variations as the basis for evolution. Darwin's "chance variations" must be single variations, not individual variation, due to the later being ever-present (pp. 35-36). De Vries did consider himself opposed to Wallace, however, whose lack of caution and pluralism had resulted in a "compact, clear and surprisingly simple" theory based on only natural selection of individual variation (pp. 40-41). Later in the book, de Vries argues that Darwin's work had allusions to what he called mutation periods, see pp. 206-208.

<sup>250</sup> Ibid., p. 575.

difficult; most of the time a scientist or horticulturist discovered them afterward. Because they happened by chance and without direction, and not by the directive actions of the breeder, they could be detected only if that breeder were on the hunt for them, of which he cited numerous examples.<sup>251</sup>

The major work of natural history that de Vries pointed to as evidence of mutation was that of the French botanist and taxonomist Alexis Jordan. A critic of Linnaeus, Jordan was a splitter, not a lumper, and distinguished 200 species of *Draba verna*. Given that Linnaeus had considered these forms one single species, it followed that the differences between these 200 so-called “elementary species” “may be very slight and often only visible to the initiated.” Indeed, they “differ[ed] less from each other than extreme variations in the same characters usually do in other plants.”<sup>252</sup> However, they were “perfectly constant,” a constancy that could “only be proved by cultivating the plants by seed.”

Indeed, these slight differences, *mutations*,

also entailed overlapping variation: depending on external conditions, such as nutrition, the variation within character of one elementary species could be both smaller and larger than another species’ character. However, elementary species differed from each other in more than a single character, so unlike Darwin’s view of species, there were no transitional forms between them. They could only be truly identified by the “test of cultivation.”<sup>253</sup>

He also cited the work of Davenport and Blankinship, which showed that “in the case of *Typha latifolia* and *angustifolia*, the curves describing their various characters overlap.” From this and other examples, de Vries concluded that Linnean species were arbitrary collectives, “mixtures,” just like genera and phyla, and explained why it had been impossible to witness the appearance of a new species: Linnean species were too large of a jump! De Vries’ sudden mutations or saltations were therefore small, even if they included multiple characters. This experimental-based definition of species overstepped “the species problem” which had proved to be an obstacle to the experimentalization of

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<sup>251</sup> Ibid., pp. 189, 195.

<sup>252</sup> Ibid., 55-56.

<sup>253</sup> Ibid., pp. 58-59.

evolution.

The student of morphological and historical evolution is concerned with the origin of the Linnean or collective species, genera, families and larger groups. The student of experimental evolution is concerned with the origin of elementary species, or rather with the origin of specific characters.<sup>254</sup>

Therefore, de Vries made evolution visible not through large leaps, but by tests of cultivation.

De Vries' distinction between fluctuations and mutations had much broader implications: a new definition of species, a different role for selection, the introduction of mutation as a creative force in evolution, and as his followers would reveal, new methods of breeding and controlling evolution.

Mutation solved the problem of regression, for they arose "independent of selection." De Vries claimed that "...species have arisen from one another by a discontinuous ... process. Each new unit, forming a fresh step in this process, sharply and completely separates the new form as an independent species that from which it sprang. The new species appears all at once; it originates from the parent species without any visible preparation, and without any obvious series of transitional forms." The essence of the mutation theory was that "species have arisen after the manner of so-called spontaneous variations."<sup>255</sup>

In contrast to these sudden, distinct, random, and non-directional mutations, fluctuations conformed to Quetelet's laws. They were always present, grouped around a mean, and were "perpetual," "gradual, continuous, reversible, [and] limited." Fluctuations were linear in that they increased or decreased a given trait ("plus" or "minus" variation), but did not produce novelty. While selection of these variations was

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<sup>254</sup> Ibid., p. 211.

<sup>255</sup> Ibid., pp. 3, 165. De Vries' mutations were of a different quality than that of the later Mendelians. The Mendelians tended to think that a mutation affected a single character, or perhaps a few, whereas de Vries held mutations to effect change throughout the entire organism (in "all their organs and peculiarities"), but were due to "the expression of a single character, a single unit..." Ibid., p. 57. The Mendelians also adopted a hardline position that fluctuations were not at all inherited, whereas de Vries believed they were, but subject to regression. The key for later developments then, as Stoltzfus and Cable argue, is that the Mendelians adopted de Vries' critique of selection and some of the basic schematics of his mutation theory, but slightly reinterpreted each of its key terms.

responsible for “the origin of many improved races” in agriculture, fluctuation’s response to selection was governed by Galton’s laws of regression, preventing species change.

From this distinction, de Vries constructed a new theory of evolution and selection. Selection-of-fluctuations followed what his experiments had shown: increase or decrease of a given trait followed by regression. With mutations, selection’s role was to sort between them: “the struggle for existence chooses from among the mutations at its disposal those which are best adapted at the moment.” The units were not individuals within a species, but the elementary species themselves, and therefore, natural selection did not “create” species, but “eliminated” them. Because mutations were random with respect to their adaptiveness,

we see therefore that in the process of the origin of new species some certainly do arise which are not capable of existence for any length of time. Nature does not confine herself to producing just what is wanted; her creative power seems to be almost unlimited. She furnishes every possibility, so to speak, and leaves it to the environment to choose what suits it. In other words mutability is indiscriminate.<sup>256</sup>

From another set of experiments, de Vries explained local adaptation as well as Lamarckian claims of the inheritance of acquired characters: they were fluctuations. In 1899, he published an experiment with a “monstrous” subspecies of poppies (*Papaver somniferum polycephalum*) that had up to 150 supernumerary carpels. He experimentally determined that the variability in carpel number was entirely dependent on its conditions, “the more favorable the conditions the more numerous the supernumerary carpels.” But in addition to this trait, better conditions were correlated with stronger plants in thickness of stem, total height, and fruit weight. Therefore, selection for a larger carpellary crown or a stronger plant is “merely a selection of the most highly nourished.” Reverse selection produced reverse results. To de Vries, the growth of the monstrous carpellary crown under selection “would be called an acquired character in the usual acceptance of the term.” Furthermore, he held that due to parallel experiments in other plants, a “universal and very important principle” (but with some exceptions) was “the simultaneous influence of the conditions of life on the visible character of an organism and on its germ

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<sup>256</sup> Ibid., p. 506.

cells. In other words we may say that selection is the choice of the best nourished individuals.”<sup>257</sup> De Vries’ solution to the Lamarckism problem, therefore, was to relegate acquired characters to fluctuations and the origin of specific characters to mutation.<sup>258</sup> The explanation was further confirmed by the transplantation experiments of Bonnier, which de Vries replicated with *Othonna crassifolia*, showing that growing plants in different environments produced adaptive ranges of variability.<sup>259</sup> Furthermore, these curves were broader in wild populations of *Chrysanthemum segetum* than in descendants of a single individual sown in a field, despite having the same mean.<sup>260</sup> That is, a mixed population was more adaptable than a single individual.

Therefore, acquired characters and localized adaptations were merely fluctuations. Indeed, following his experiments, he pointed out that “nutrition ... is at the bottom of all individual variability.” This identity was further indicated by so-called acquired characters’ inheritance being subject to Galtonian regression following selection. Therefore, “selection consists in the choice of the most highly nourished.”

As mentioned above, de Vries’ theory of evolution consisted in two parallel processes that were formerly considered one. Their relationship was that mutations produced new means, “on both sides of which fluctuations may occur.” Thus, “constancy and variability are perfectly compatible.”<sup>261</sup> Their evolutionary differences were that:

On the one hand the struggle takes place between the individuals of one and the same elementary species, on the other between the various species themselves. The former is a struggle between fluctuations, the latter between mutations.<sup>262</sup>

The former produced “local races,” explained acclimatization, and was subject to regression. But,

The natural selection of newly arisen elementary species in the struggle for existence is an entirely different matter. They arise suddenly and without any obvious cause; they

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<sup>257</sup> Ibid., p. 142.

<sup>258</sup> Ibid., p. 143.

<sup>259</sup> “Far too little attention has been paid to the relation between the range of variation of the individual characters and the degree of their adaptation to changing conditions of life; and the whole matter is still very much of a mystery. Here again it is probable that further study will tend to emphasize the fundamental distinction between variability and mutability.” p. 154.

<sup>260</sup> Ibid., pp. 151-152.

<sup>261</sup> Ibid., p. 518.

<sup>262</sup> Ibid., pp. 211-212.

increase and multiply because the new characters are inherited. When this increase leads to a struggle for existence the weaker succumb and are eliminated.<sup>263</sup>

But natural selection did not create species in either cycle: selection of fluctuations did not lead to speciation; selection between mutations was selection between species. “The rôle played by natural selection in the origin of species is destructive, and not a constructive one.”<sup>264</sup> Rather, mutations were evolution’s creative force.

The theoretical results of de Vries’ natural history, statistical analysis, and experimentation indicated how to take control of evolution, although for the moment, his views were more deflationary than productive. His refashioning of selection imposed limits: “all that he [the breeder] can do by selection is to intensify the produce and yield of characters already present; but so far it is not within his power to call into existence new characters.” Hybridization was a halfway measure towards creating “new forms.” For new characters, scientists had to develop an “experimental physiology of the origin of species” that would allow for “control over much that at present seems beyond our reach.” Specifically, once “the breeder has obtained control over variability, why should he not obtain it over mutation as well?” Inducing “mutations at will” would likely take “a long time,” however. Until then, mutations “must be waited for.”<sup>265</sup>

Throughout the book, de Vries called for further investigations; his theory was to be a launchpad for research, not a final resolution. He called for more demonstrations of Quetelet’s law, particularly across generations. He was interested in an explanation for polymorphic curves (as Pearson and Weldon were puzzling out), which he suggested would be due to “mixtures of perfectly distinct elementary species growing together or to the existence of antagonistic characters within the limits of a single species” (e.g., annual vs. biennial forms). He called for more work on correlative variation, ecology and growth, and the workings of artificial selection with respect to regression. He also advocated for work that could contradict his theory, such as a selection experiment that began with seed-parents small, weak, and pale and tried to create “apetelous, fruitless,

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<sup>263</sup> Ibid., p. 212.

<sup>264</sup> Ibid., pp. 211-212.

<sup>265</sup> Ibid., pp. 57-58, 186, 306, 33. Calls for the control of evolution are scattered throughout the book, see. pp. 164, 167-168, 207.

glabrous, spineless, white-flowered, unisexual or sterile plants,” i.e., could selection push an elementary species beyond its limits? All of this was to “aim at ... a complete control of variation. We must become so thoroughly acquainted with the underlying factors that we can predict the results of our experiments.”<sup>266</sup> What de Vries had done was provide “the proof ... that this phenomenon can be dealt with experimentally.”<sup>267</sup>

As de Vries would say in his public address at the opening of the Station for Experimental Evolution in Cold Spring Harbor (discussed in the following chapter), he thought evolutionary science had important applied implications for society, particularly with regard to agriculture.<sup>268</sup> While he always thought science would ideally remain “pure,” with applications following automatically, he consistently reported to the public and to agriculturists/horticulturists the latest developments in the botanical sciences.<sup>269</sup> (Recall though that de Vries’ own work was partially derived from practical and applied work in breeding.) The distinction between fluctuating variation and definite mutations was key to improving crops, he thought. More important for de Vries was the potential control of mutations: he lamented that they “occur frequently, but always by chance,” and that a primary goal for science was “to try and free the practice from this dependence on chance.”<sup>270</sup> (Theunissen notes that by the end of his life, he had to admit defeat.) These close ties between theory and practice de Vries believed were fundamental to social progress, one achieved through the “close, noble alliance of capital and science.”<sup>271</sup> Such work would be mediated by the universities, which he thought should “cultivate the most intimate connection between theory and practice, between abstract science and actual life.” In a more excited moment, he declared: “New races and also new species! This will

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<sup>266</sup> Ibid., pp. 159-164.

<sup>267</sup> Ibid., p. 497.

<sup>268</sup> De Vries also drew eugenical, or anti-eugenical, conclusions from the mutation theory. In essence, he believed that human races, like animals and plants, were stable and not undergoing a mutation period, and were thus not amenable to improvement via selection or through changes in environmental conditions. For more on his beliefs, see Theunissen, “Knowledge Is Power,” 308–11.

<sup>269</sup> Theunissen usefully points out that de Vries’ fellow champion of control, Jacques Loeb, who was also trained by Julius Sachs, had a different perspective. Loeb was a follower of Ernst Mach and much less interested in structural explanations (as opposed to de Vries’ drive to understand variation and heredity physiologically). Loeb also saw no distinctions between pure and applied science, whereas de Vries did. Theunissen.

<sup>270</sup> Quoted in Theunissen, 304.

<sup>271</sup> Hugo de Vries, “Kapitaal En Wetenschap,” *Album Der Natuur* (1898): 353–66.



henceforth be our slogan, first for science, but then also for practice, for the flourishing of agriculture and the prosperity of all nations!”<sup>272</sup>

### Conclusion

Experimental evolution began in the nineteenth century rife with challenges, but its motive forces – understanding, control, experimentation, profit – drove it forward. This was not the story of a new method arriving on the scene and taking science by storm. Even some of its apparent achievements, such as Dallinger’s instrumentation or Weldon’s statistical methods, did not initiate long-term growth or the establishment of a new research program. Yet its core questions animated further work. Darwin, Mendel, Dallinger, Weldon, and de Vries all wrestled with how to extrapolate the artificiality of experimentation to the natural world. Darwin and Mendel (and Bateson) did not see much of a distinction at all — indeed, Darwin considered artificial selection of livestock a detectable and simple version of natural selection on wild animals. Dallinger, on the other hand, was reluctant to extrapolate even to other individuals of the same species, although he did provide a couple of general conclusions. Weldon articulated a program intended to avoid the artificial entirely, but the practice of his theory could not solve the problems he set out to research, and thus, he reluctantly conducted experiments, mimicking the crabs’ changed environment by design. Hugo de Vries also traveled between nature and artifice but cautioned against unconditional use of breeders’ work, arguing for experimentation, but not in lieu of natural history. In this way, de Vries was remarkably Darwinian, whereas Weldon was not.

Weldon and de Vries were far more involved in theoretical disputes over the relative powers of evolution’s forces and the nature of variation and heredity, the former particularly due to new practical advances of statistics. These theoretical debates were in part fueled by the search for patterns in a wider range of organisms, beyond pigeons, cattle, and sheep, and especially for de Vries, in the plant kingdom. By this time science had taken evolution as a fact, and both Weldon and de Vries considered it visible, although by different methods and for different reasons. However, de Vries’ influence was far more lasting and significant — not only did he produce a different theory rooted

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<sup>272</sup> Quoted in Theunissen, “Knowledge Is Power,” 300, 303–4.

in different practices, but he also brought the question of power and control to the forefront. Weldon, like Darwin, was not particularly interested in making evolution controllable and useful, reflected in his theory and his practice; de Vries, like Darwin, thought the de facto control of evolution was an important well of information. It was up to him and the following generation, however, to develop practice as accumulated theory and theory as accumulated practice.

Among nineteenth-century biologists, Weldon, a professor and journal editor, was in the best position to institutionalize an experimental evolution, but his research program and the controversy it engendered, perhaps causing an early end to his life, prevented him from training a new generation to follow in his footsteps. The statistical methods he helped develop would leave a lasting impact as biologists continued to train with Karl Pearson, however. De Vries also did not establish a program, but *Die Mutationstheorie* took the world of evolutionary science by storm. This was particularly so in the United States, where the theoretical and the practical (experimental) were of interest to wealthy patrons looking to help develop an independent American science.<sup>273</sup> As Sharon Kingsland notes, de Vries' emphasis on control "served as vehicle to attract the patron's interest to the scientific enterprise, an enterprise that would invigorate American research and contribute to the wealth of the nation. De Vries was shrewd enough to understand Americans' pride in their independent development of science." It also tapped into the mood among biologists for experimentation, particularly Daniel MacDougal and Charles Davenport, soon to be directors of Carnegie Institution of Washington experiment stations. De Vries helped convince the wealthy to fund work that would make evolution visible, controllable, and useful.

As my next chapter will show, it took a set of ambitious biologists — particularly Charles Davenport, an early biometrician — to lobby a capitalist philanthropy to build and fund a permanent research station dedicated exclusively to the experimental study of evolution and biology. This station funded by Andrew Carnegie, combined with a growing consensus that experimentation was the path forward on the heels of *Die Mutationstheorie* and Mendel's rediscovery, provided the firm base upon which

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<sup>273</sup> Sharon Kingsland, "The Battling Botanist: Daniel Trembly MacDougal, Mutation Theory, and the Rise of Experimental Evolutionary Biology in America, 1900-1912," *Isis* 82, no. 3 (1991), 491.

experimental evolution could emerge. The Station would soon house the Eugenics Record Office as it also became a birthplace of hybrid corn, further signs of the dominating forces of capitalism in experimental evolution as a dialectic between nature and society.

### Chapter 3:

#### A New Atlantis: The Station for Experimental Evolution (1890-1920)

##### The Need for an "Institut Transformiste"

In the wake of nineteenth-century experimental evolution, biologists recognized the need for a well-financed institution that could conduct long-term experimentation, commit to a program that tested theories and hypotheses, and house several scientists: a *station* for experimental evolution. I briefly discuss the various calls that scientists made for such an institution and then examine at length the Station for Experimental Evolution at Cold Spring Harbor. I analyze Charles Davenport's extensive application materials to the Carnegie Institution of Washington to understand his broad vision for the endeavor, and then follow its first fifteen years of existence through 1920, when it was reorganized as the Department of Genetics. Hugo de Vries also reappears to articulate his vision of experimental evolution at the Station's grand opening in 1904. I show that the Station's work was incredibly broad, perhaps engaging in too many projects at once. But through its direct work and its grants, it was a central organizing force for American experimental evolution that helped bring Mendelism and mutationism to the fore. While Darwin, Mendel, and de Vries dialectically integrated theory and practice as individuals, the Station did so as an institution, only possible due to the interest from capital to take control of evolution.

In 1890, French biologist Alfred Giard lectured before the Sorbonne on Lamarckian evolution, challenging Darwin's methods of "experimentation," signaling the professionalization and increasing standardization required by biological science:

If evolutionists must content themselves in most cases with experiments unconsciously carried on in Nature, or those of breeders, instead of applying themselves to verifications made with all the rigour of modern scientific precision, is it not because of the deplorable insufficiency of our laboratories? One is astonished that in no country, not even where science is held in greatest honour, does there yet exist an *instiut transformiste* consecrated to the long and costly experiments now indispensable for the progress of evolutionary biology.<sup>274</sup>

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<sup>274</sup> Originally published on December 5, 1890 in *Revue scientifique*, the article was translated into English and published as Alfred Mathieu Giard, "The Principle of Lamarck and the Inheritance of Somatic Modifications," *Nature* 43, no. 1110 (February 5, 1891): 331.

In 1891, Darwin's disciple George John Romanes proposed such a station to Oxford University, quoting Giard and providing brief commentary with a budget. Believing England to be "the natural territory of an establishment of this character," he suggested a two- to three-acre plot housing three residents — a naturalist, a gardener, and a keeper —, as well as animals.<sup>275</sup> (This was reminiscent of Bakewell's Dishley Grange.) He circulated this letter to fellow biologists, but Romanes' English *Institut transformiste* was not to be.

Also in 1891, the French zoologist Henry de Varigny called explicitly for an "experimental evolution" — the term's first documented use — in a series of lectures at the Summer School of Arts and Sciences in Edinburgh.<sup>276</sup> He thought experimental work could demonstrate the reality of evolution in real time, so as to convince special creationists that Darwin was generally right. De Varigny also argued that turning evolution experimental would help biologists advance a science bogged down by competing speculative theories. Pointing to breeders as a kind of 'experimental evolutionist,' de Varigny claimed practical and economic benefits would result.

To launch an experimental evolution, de Varigny, echoing Giard and Romanes, suggested the construction of an "institution of some sort," that would have "extensive grounds, a farm with men experienced in breeding, agriculture, and horticulture, some greenhouses, and a laboratory with the common appliances of chemistry, physiology, and histology."<sup>277</sup> Such a station would allow for long-term experiments. It would be akin to an agricultural research station, but not devoted solely to practical questions, reflecting a commitment to discovering laws with organisms most useful to the task. It would thus mediate between agricultural and capital needs and the scientific understanding of nature.

Not every biologist agreed with Giard and de Varigny. Liberty Hyde Bailey, the American horticulturist, followed Darwin in believing that the work of breeders was sufficient to demonstrate the reality of evolution. After listing a bounty of examples of radically changed forms in the plant kingdom under domestication, Bailey argued in

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<sup>275</sup> George John Romanes, "An Institute Transformiste," in *The Life and Letters of George John Romanes* (London: Longmans, Green, and Co., 1896), 268–71.

<sup>276</sup> Henry de Varigny, *Experimental Evolution* (London: Macmillan and Company, 1892).

<sup>277</sup> de Varigny, 256; Romanes, "An Institute Transformiste," 285–87.

“Experimental Evolution Amongst Plants,”

He [everyone] knows that nearly every plant which has been long cultivated, has become so profoundly and irrevocably modified that people are disputing as to what wild species it came from. It is immaterial whether they are called species or varieties. They are new forms. Some of them are so distinct that they have been regarded as belonging to distinct genera. Here is the experiment to prove that evolution is true, worked out upon a scale and with a definiteness of detail which the boldest experimenter could not hope to attain, were he to live a thousand years. The horticulturist is the only man in the world whose distinct business and profession is evolution. He, of all other men, has the experimental proof that species come and go.<sup>278</sup>

According to Bailey, Huxley’s critique of Darwin – that biologists needed to show the formation of a new species to prove the truth of evolution – had, in fact, been answered thousands of years prior and continued to be demonstrated in his own time. Even though these were not strict experiments by modern standards, Bailey thought his examples (i.e., most fruits, vegetables, and nuts) and the profit they produced proved his point. But for scientists interested in *causes*, Bailey’s argument held no water. Giard, Romanes, and de Varigny were to be proven correct: long-term and steady experimentation of evolution was required to understand how it worked.

### **Lobbying a Robber Baron’s Philanthropy**

While the European proposals for experimental institutions dedicated to evolution failed, Charles Davenport lobbied the Carnegie Institution of Washington (CIW) to construct one in 1904 at Cold Spring Harbor, New York: The Station for Experimental Evolution. Through the Station, Davenport sought to “realize that dream of [Francis] Bacon, who saw in the New Atlantis, gardens devoted to the experimental modification and improvement of animals and plants.”<sup>279</sup> In this chapter, I explore Davenport’s vision for experimental evolution and analyze the Station’s work through 1920 (when it became the Department of Genetics). Davenport’s vision was all-encompassing, reflected by the Station’s wide-ranging and contradictory research, and demonstrated the need for

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<sup>278</sup> Note that Bailey specifies the horticulturist, in line with de Vries in *Mutation Theory*. Bailey, “Experimental Evolution Amongst Plants,” *The American Naturalist* 29, no. 340 (1895): 318–25.

<sup>279</sup> CIW Yearbook, Vol. 3, 1904, p. 33. CIW yearbooks are published the January of the following year of the report. For the sake of clarity, my citations reflect the year the report covers, not its publication date.

significant capital to carry out the research program. The resonance between capitalism and experimental evolution that had begun with Bakewell and Darwin continued to be key to the latter's historical development and potentially the former's expansion into the agricultural sector.<sup>280</sup>

Charles Davenport, like many of his contemporaries, began his scientific career as a zoological morphologist, but became convinced that the future of biology was experimental, quantitative, applicable, and causally focused. He began by integrating the statistics developed by Pearson and Weldon into his morphological research, which rendered evolution *visible* and possibly predictable. The shape and skew of the curves produced by biometry were themselves shaped by "the direction of evolution." Weldon's crab work, according to Davenport, produced "beautiful results," and refuted the belief that "we should not expect in man's brief lifetime, nor even within historic times, to find such changes [in racial differentiation in nature]." Evolution remained invisible if biologists relied on "adjectives for specific description," but with quantitative methods, "we can hope soon to prove that many species are undergoing change and to determine the cause of the change."<sup>281</sup> The rapid adoption of quantitative methods by a wider swath of biologists was leading to the "discovery" of "the role of natural selection, the method of evolution and the laws of inheritance, especially where combined with experimentation."<sup>282</sup> Although biometry did not itself address causes, it was "the key to the first door that has barred true progress in the difficult subject of the origin of organic diversity."<sup>283</sup> Statistics

will enable us to measure precisely the results of any change in environment, artificially or naturally brought about. We shall thus be able not only to tell what are the factors of phylogenetic change, but also the rate of such changes. We shall get possession of the laws of evolution so that we can not only reconstruct the past, but also predict the future

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<sup>280</sup> I briefly address the historiographical debate over the impact of biology on agriculture in the Conclusion.

<sup>281</sup> Davenport 1899, p. 271. Already Davenport was becoming interested in the control of evolution, writing that "the quantitative studies made on the result of experiments to produce race change will be the most striking. In fact, in its application of combined experimental and statistical methods to genetic problems, zoology will reach its highest development." p. 272. (He reiterated a similar point in 1901, p. 448.)

<sup>282</sup> Davenport, "A History of the Development of the Quantitative Study of Variation," *Science* 12, no. 310 (1900): 870.

<sup>283</sup> Davenport, "The Statistical Study of Evolution," *Popular Science Monthly* 59 (1901): 457–58.

development of a race.<sup>284</sup>

Davenport also began to emphasize experimentation and control after the rediscovery of Mendel's laws (1900) and Hugo de Vries' publication of *The Mutation Theory* (1901). He argued that "prominent among the advances of the [twentieth] century will be the ability to control biological processes," including the "direction of ontogeny and of phylogeny." "The morphologist will more and more consider experiment a legitimate method for him."<sup>285</sup> Davenport therefore sought to synthesize the methods of the major competing theoretical trends.

Davenport recognized that a program of experimental evolution required a dedicated institution with a stable source of funding. The Carnegie Institution of Washington (CIW) was the perfect patron, launched in 1902 with a \$10,000,000 endowment from the captain of the steel industry. Before the development of extensive public funding, Carnegie (and Rockefeller and Ford) provided a niche for scientific visionaries and organizers such as Davenport. Biologists took advantage of what public funding existed in the agricultural sciences, but the requirements of immediate application prevented what Davenport considered to be the scientific need to discover laws. This is exactly what CIW was looking to fund.

Independent of Davenport, Roswell H. Johnson also submitted a brief proposal for a "vivarium" to CIW.<sup>286</sup> Published alongside Davenport's proposal and Whitman's "biological farm," Johnson himself noted that, "I remember that Professor Davenport in his course on evolution at Harvard made a strong plea for experimental work."<sup>287</sup> In

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<sup>284</sup> Davenport, 459–60.

<sup>285</sup> Davenport, "Zoology of the Twentieth Century," *Science* 14, no. 348 (1901): 317.

<sup>286</sup> Roswell Hill Johnson, "Biological Experiment Station for Studying Evolution," in *CIW Yearbook*, vol. 1 (Washington, D. C.: CIW, 1902): 274–80. He also published a condensed version as "The Carnegie Institution," *Science*, 1902, 987–990. Johnson told Davenport in June 1902 that he had written to a CIW trustee to gauge the institution's interest. He also thought the University of California could establish one. Johnson to Davenport (1902/6/13), APS Davenport, Box 59, "Johnson, Roswell H.," folder 1.

<sup>287</sup> Whitman's proposal was an edited excerpt from "A Biological Farm: For the Experimental Investigation of Heredity, Variation and Evolution and for the Study of Life-Histories, Habits, Instincts and Intelligence," *The Biological Bulletin* 3, no. 5 (1902): 214–24. He hoped it would be built at Woods Hole. Whitman emphasized that a station would not only allow for long-term experimentation, but long-term observation: "The functions of a biological farm are not all summed up in experimentation. That old and true method of natural history — observation — must ever have a large share in the study of living things. Observation, experiment and reflection are three in one. Together they are omnipotent; disjoined they become impotent fetiches. The biology of to-day, as we are beginning to realize, has not too much laboratory, but too little of



contrast to Davenport's emphasis on control, Johnson emphasized the need for experimental hypothesis testing. He considered "nearly all of the post-Darwinian writing" to be "largely deductive" or too "static" (biometry). Instead, "evolution, above all, requires dynamic studies" of "selective life values of different variations, inheritance of acquired characteristics, environmental alterability of the germ-plasm; modification preventing death under adverse conditions, etc." His suggested experiments included the isolation of two populations to determine whether their traits regress to the mean or diverge and testing selection by subjecting shrimp to fresh water. He even proposed a test for "organic evolution" (the Baldwin effect) using camouflaging tree frogs. Other experiments could test "fecundal selection," "sport prepotency," assortative mating, correlations, and the existence of determinate variation. He emphasized institutional needs, noting that experimental evolution "has hardly begun" due to the expense, time, and permanence required. It would benefit from an experimental station that hired workers to carry out routine labor using superior equipment and infrastructure constructed for the tasks directed by resident scientists, much like the agricultural experiment stations. Johnson estimated the startup costs to be \$10,000 (including a barn, greenhouse equipped with aquaria, and a laboratory) with \$6,300 annually for maintenance. David Starr Jordan, one of America's leading biologists, commented that Johnson's proposal was "extremely desirable."<sup>288</sup>

Davenport's first – and unsuccessful – proposal was like Johnson's. He declared such a station's aims to be "the analytic and experimental study of the causes of specific differentiation—of race change." The methods of study included crossbreeding to study "laws and limits of inheritance," "the experimental production of variation" via hybridization or changes in external conditions, biometrical investigations of geographic distribution and isolation, as well as selection experiments aimed at "the origin of adaptation of organisms." He also cited the previous proposals of Whitman, Romanes,

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living nature. The farm will certainly do much to mend this great deficiency." CIW considered Woods Hole "impracticable" (CIW Yearbook, Vol 3, 1904, p. 22).

<sup>288</sup> Roswell Hill Johnson, "Biological Experiment Station for Studying Evolution," in *CIW Yearbook*, vol. 1 (Washington, D. C.: CIW, 1902): 274–80. He published a condensed version as "The Carnegie Institution," *Science*, 1902, 987–990. Johnson told Davenport in June 1902 that he had written to a CIW trustee to gauge the institution's interest. He also thought the University of California could establish one. Johnson to Davenport (1902/6/13), APS Davenport, Box 59, "Johnson, Roswell H.," folder 1.

and de Varigny. He proposed the site of Cold Spring Harbor, estimating startup costs at \$36,000 with annual expenditures of \$9,000. CIW did not find either application worthy.

Davenport's second and successful application was exhaustive and demonstrated his broad vision of experimental evolution's future. Noting a visit to "many of the principal experimental evolutionists of Europe," Davenport urged to CIW that "more than ever is the importance of an experimental station felt where quantitatively exact experiments in breeding through many generations can be conducted and from which material can be supplied to various specialists for cytological and biochemical investigation."<sup>289</sup> With his application, discussed in the following section, Davenport included "a summary of progress in experimental evolution," a "statement of eight experiments which it is desired to start as soon as assistance is granted," a promised lease from the Wawepex Society of Cold Spring Harbor to grant CIW the required land, and an estimated budget of \$7,500. Its purpose would be to

Study the laws of inheritance of ontogenetic + phylogenetic variation. ... Study the adjustment of organism to conditions (adaptation) whether by self-adjustment; survival of the fittest individuals or segregation in the fittest environment.<sup>290</sup>

### **Davenport's Vision**

Davenport's application materials, along with lecture notes dating from this period, demonstrated a broad vision of what experimental evolution could be, embedding it within a history of science so as to convince CIW that they would not be funding a novelty, but contributing to the next stage of scientific progress. Notably, given that Davenport and the Station for Experimental Evolution are historically associated with eugenics, the application materials do not contain any mention of allusion to eugenics whatsoever. Instead, Davenport's initial interests remained almost exclusively among the zoological and botanical, eugenics emerging afterward.

In his "summary of progress," Davenport echoed de Varigny, stating that evolution had been demonstrated, but scientists had yet to "learn its method." He wrote,

With the modus operandi of evolution the case is quite different. Indeed, we have

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<sup>289</sup> Davenport to the Trustees of the Carnegie Institution (1903/3/5), APS Davenport, Series II, Box 100, "Davenport, C.B. To Executive Committee of C. I. W., 1904" folder. Davenport did not note who these "principals" were.

<sup>290</sup> APS Davenport, Series I, Box 37, "Experimental Evolution Lectures" folder 1.

practically no satisfactory cases where the process has been carried through. Only by following through a case of evolution under perfectly known conditions can we hope to learn the method. This, then, is what is required; a place to study the conditions under which evolution takes place--a Station for the experimental study of evolution. The importance of such a Station has long been recognized.<sup>291</sup>

Davenport's history of experimental evolution began with Francis Bacon, who in *New Atlantis* (1627) "recognized not only the possibility of modifying species but also the importance of studying the laws of such modification."<sup>292</sup> He speculated that Bacon may have drawn inspiration from Japan (via Dutch sailors), where "more than in any other country, experimental breeding has been carried on, in a half curious, half commercial spirit. ... Examples of this Japanese art are now familiar to us: such are the chrysanthemums, dwarf trees, double-tailed gold fishes, and long-tailed poultry."<sup>293</sup> Bacon also envisioned the "House of Solomon," an institution of orchards, gardens, parks, enclosures, ponds, and buildings dedicated to the modification and breeding of plants, livestock, and insects.<sup>294</sup>

According to Davenport, "the ideas of Bacon lay long latent, as did the evolutionary doctrines of the Greeks," until Lamarck, who "founded a French school of evolutionists in which this suggestion [experimental evolution] arose again," primarily through Isidore Geoffroy Saint Hilaire (the son of Étienne Geoffroy).<sup>295</sup> Davenport quoted from the younger Geoffroy's work, *Histoire naturelle générale des règnes organiques*, in which he stated:

Since Nature left to herself never exhibits great changes in the conditions of existence it is clear that there is left us only one method of seeing such changes and of determining their effects upon the organism. *We must oblige nature to do what she will not do spontaneously.*

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<sup>291</sup> Davenport to the Trustees of the Carnegie Institution (1903/3/5), APS Davenport, Series II, Box 100, "Davenport, C.B. To Executive Committee of C. I. W., 1904" folder.

<sup>292</sup> APS Davenport, Series I, Box 37, "Experimental Evolution Lectures" folder 1.

<sup>293</sup> APS Davenport, Series II, Box 100, "A Summary of Progress in Experimental Evolution."

<sup>294</sup> Bacon in *Sylva Sylvarum* also promoted the methods of hybridization and transplantation, the latter of which would inspire Davenport's contemporary Lamarckian experimentalists. Davenport did not mention this work.

<sup>295</sup> APS Davenport, Series I, Box 37, "Experimental Evolution Lectures" folder 1.

To take control of evolution, Geoffroy promoted Bacon's own methods of modification, whether through environmental or dietary changes, and "to introduce an element with which, unhappily we cannot dispense, namely, time."<sup>296</sup>

Davenport surveyed the prior calls to establish a station dedicated to experimental evolution. He mentioned that Darwin "seems to have undertaken no [experiments] nor to have urged the importance of an experimental station for the purpose." Instead, "the post-Darwin revival of effort in this direction seems to have been due to ... [the] Frenchman Giard." Here Davenport discussed Giard, Romanes, and de Varigny. Davenport also noted that the Royal Society of London's Committee on Evolution, chaired by Francis Galton (the "father of scientific methods of investigating evolution"), had also discussed such a station. Herbert Spencer, a member, corresponded with Andrew Carnegie, but "these efforts bore no immediate fruits and since these rebuffs the plan for a great Evolution Station have lain dormant in England." In Germany, "likewise, the money has not been forthcoming." Turning to America, Davenport discussed Whitman's idea of a "lake biological station." Whitman wrote in 1892,

Such a station has been nowhere provided but its need has been felt and acknowledged by the foremost biologists of today. There are no problems in the whole range of biology of higher scientific interest or deeper practical import to humanity than those which center in variation and heredity. For the solution of these problems, and a thousand others that turn upon them, facilities for long-continued experimental study, under conditions that admit of perfect control, must be provided.<sup>297</sup>

Davenport quoted from his own 1897 lecture to the American Society of Naturalists, in which he said,

The reason why they [variation and heredity] have not been worked upon is largely because they don't lend themselves to investigation in the laboratory. For the successful study of these problems one needs, indeed, not an ordinary laboratory, but a farm or an extensive zoological reserve with hothouses, breeding ponds, insectaries and vivaria of various sorts. With such means at his disposal a naturalist might hope, during a long series of years, to answer many of these fundamental phylogenetic questions.<sup>298</sup>

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<sup>296</sup> Quoted in APS Davenport, Series II, Box 100, "A Summary of Progress in Experimental Evolution."

<sup>297</sup> APS Davenport, Series II, Box 100, "A Summary of Progress in Experimental Evolution." Underline original. I cannot locate the original document, but this quotation reappeared in Charles Otis Whitman, "Some of the Functions and Features of a Biological Station," *Science* 7, no. 159 (1898): 37–44.

<sup>298</sup> APS Davenport, Series II, Box 100, "A Summary of Progress in Experimental Evolution."

For a science dedicated to controlling evolution, a continuing concern among its practitioners was that it was they who were subject to nature, not only due to their lack of knowledge but also by the process itself. Concluding that “naturalists have for some time realized the necessity of an experimental station for the proper prosecution of scientific evolutionary studies,” he turned to experimental evolution’s achievements thus far, conducted “under great limitations and difficulties.”<sup>299</sup>

Davenport defined evolution as “the movement of the germ plasm,” and therefore, experimental evolution “seeks to control the rate and direction of the movement of the germ plasm.” Its purpose was “not to test truth of evolution, not to produce an example of evolution ... but to determine laws + limits of racial modification.”<sup>300</sup> For Davenport, experimental evolution was identical with the control of evolution. The language of “modification,” “induction,” “production,” and “direction” permeate his notes, implying that the elucidation of causes would provide levers of control. That is, if biologists discovered the causes of mutation, presumably the biologist could induce mutations artificially with the same agent. As Bacon had advocated for the utility of experimental philosophy, so did Davenport.

Davenport’s historical accounts also display his Baconian and Darwinian mission, blending the work of eighteenth- and nineteenth-century breeders and botanists into the history of experimental evolution.<sup>301</sup> For example, he discussed Rudolph Camerarius’ discovery of plant sexuality as well as Joseph Kölreuter’s work on hybridization. He quoted from Paul Dudley’s 1724 article in the *Philosophical Transactions* which reported that differently colored rows of maize would “mix and interchange their colors.” He listed papers by Benjamin Cooke, who crossed varieties of apple trees and maize. He considered the nurseryman Thomas Fairchild, active in the early seventeenth century, as

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<sup>299</sup> APS Davenport, Series II, Box 100, “A Summary of Progress in Experimental Evolution.” Note that Davenport made little to no distinction between naturalists and experimentalists.

<sup>300</sup> Note that Davenport’s use of “racial” refers to the biological, not the human and eugenical. APS Davenport, Series I, Box 37, “Experimental Evolution Lectures” folder 1 and 2. He noted also that experimental evolution is “not concerned with [hard to read] (embryology, ethology).

<sup>301</sup> Davenport’s theoretical history followed Osborn’s *Greeks to Darwin*, beginning with the ancients and leaping to Linnaeus and John Ray. He noted the evolutionary mechanisms advocated by Lamarck, St. Hilaire, Weismann, and de Vries.

“the first scientific hybridizer,” i.e., “the first hybridizer for material purposes.”<sup>302</sup> He concluded this historical section with Christian Sprengel, the botanist, and Thomas Knight, a horticulturist. For Davenport the history of botany and horticulture were intertwined and long had elements of experimental evolution even if the historical actors had no concept of such.

An overriding concern for Davenport was the role of the environment in evolution. Experimental evolution required a stable institution because biologists needed to control for the environmental effects that permeated an organism’s development and evolution. Since at least the days of Lamarck, and particularly during the post-Darwinian period, theories of evolution posited incommensurable roles for the environment; thus, to study evolution, the role of the environment had to be isolated and controlled. This was a problem — both theoretical and methodological — that dominated the initial decades of experimental evolution.

To illustrate “the problem of experimental evolution,” Davenport developed a nautical metaphor. Treating evolution as “the movement of the germ plasm” and adopting Weismann’s “fundamental” germ/soma distinction,<sup>303</sup> he asked,

Is this movement directed from within like the movement of a mighty ocean steamer, unaffected by the somas it throws off [just] as the path of the steamer [i]s unaffected by the spray or the foam it leaves in its wake? Does the germ plasm go thundering through the ages impelled by its own [unclear] Or is the germ plasm like a canal boat little [launch?] led hither + thither by a rope in the [unclear] of spring fastened to “environmental conditions”? Does every soma it produces sway the germ plasm to this side or that [just] as the mother sheep transformed its bleating progeny? Is the movement? of the germ plasm definitely directed like the torpedo that rushes from the warship, or is it like the clip? on the water that bobs up + down on the waves and only gets anywhere as some prevailing current causes it to drift? One or the other of these hypotheses, or both or neither is true. How can we ever find out the fact of the case?<sup>304</sup>

<sup>302</sup> APS Davenport, Series I, Box 37, “Experimental Evolution Lectures” folder 1.

<sup>303</sup> Later in his lecture notes, Davenport, at length, questioned the validity of this distinction.

<sup>304</sup> APS Davenport, Series I, Box 37, “Experimental Evolution Lectures” folder 1. Underline original. He later offered a different metaphor, likening the fate of the germ-plasm not to a “stream,” but to an “inextricable network of bayous” because of sexual reproduction (CIW Yearbook, Vol. 7, 1908, pp. 88-89).

For Davenport the key question was whether the germ plasm determined its own direction or was controlled by environmental conditions. If the latter, did the environment produce particular changes or merely increase variability? Davenport categorized theories of evolution along a spectrum in which either option made up its ends. The ocean steamer represented Nägeli, who thought “phylogenetic change is determined by an automatic perfecting principle (modified and controlled by an adaptive variation).” The canal boat represented George Henslow, who thought the environment induced definite and inheritable variation “always in the direction of adaptation to the environment itself.” That is, “self adaptation [w]as a cause of variation.” In the middle lay, from steamer (internal) to boat (external), the theories of de Vries, Darwin, Weismann, as well as the theory of organic selection (articulated by Baldwin, Osborn, and Lloyd Morgan), and Yves Delage.<sup>305</sup> Davenport concluded, “I set the problem of the modifiability of the germ plasm by extrinsic or intrinsic causes; acting directly or indirectly; definitely or indefinitely — the alterability of the amplitude of the pendulum’s swing and the change of the centre of its vibration.” Given the central role of environment, Davenport wrote, biologists should “study variation and learn the external or internal conditions with which it is correlated in nature + the conditions under which it may be experimentally be induced and controlled.”<sup>306</sup>

Not only was the environment a theoretical issue, it produced methodological problems. Because the germ plasm’s “movement” was inaccessible to observation and measurement, one had to “study the successive somas it produces one after the other.” But, because somas developed in response to environmental causes, a biologist had to find ways to standardize environmental variables. When controlled, and “if the successive somas *a, b, c, d, &c.* produced from the same germ-plasm in successive years are alike then the germ-plasm is probably undergoing no change”; but, if they are different, the germ-plasm itself is probably changing. However, it was possible that sexual reproduction produced germinal changes, so Davenport advocated the use of

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<sup>305</sup> Ibid. Henslow authored *The Origin of Plant Structures by Self-Adaptation to the Environment* (1895), who in this discussion took Lamarck’s place. Davenport intended to discuss orthogenesis, but Theodore Eimer’s name is crossed out, replaced with Delage.

<sup>306</sup> Ibid. He also emphasized the importance of studying inheritance, self-adjustment, selection, and “segregation in the fittest environment.”

“parthenogenetic and self-fertilizing” animals as well as plants that could be propagated through grafting and cutting. In addition, biologists should study characters that seemed the most independent of environmental influence.<sup>307</sup> Thus the environment, or external conditions, caused a host of entangled problems that biologists spent years working to resolve.

Even with Davenport’s organismal recommendations, what was striking about Davenport’s vision, and as experimental evolution developed, was the breadth of topics and organisms under study. Referencing William Bateson’s 1894 *Materials for the Study of Evolution*, Davenport lectured on surveys of variation throughout all the zoological phyla, noting whether scientists had discovered mutations, fluctuations, and environmental effects.<sup>308</sup> As noted above, he integrated the history of plant breeding (but curiously little on animal breeding) into his history of experimental evolution, but his proposed experiments, discussed below, included spiders, ladybird beetles, goats, and cats. Historical examples featured poultry, sparrows, butterflies, crabs, scallops, and apple trees. Before the reign of *Drosophila* and *E. coli*, experimental evolution reflected its roots in natural history, botany, entomology, and zoology, as well as the practical arts of horticulture and agriculture.

In his “Summary of Progress in Experimental Evolution,” which he submitted to CIW as part of his application, Davenport categorized previously conducted experiments into eight classes: (1) the statistics of variation and selection, (2) the effects of domestication and multi-generational captivity, (3) the inheritance of acquired characters as well as self-adjustment/plasticity, (4) the existence and fate of sports in breeding and in the wild, (5) telegony, (6) intra-specific crossing, (7) inter-specific hybridization, and (8) the effects of isolation.<sup>309</sup>

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<sup>307</sup> Ibid. He framed somas as “our index of the qualities of any germ-plasm... Each soma is the biological analysis of its germ-plasm.” Environmental variation and dominance produced “error” (CIW Yearbook, Vol. 7, 1908, pp. 86-87).

<sup>308</sup> APS Davenport, Series I, Box 37, “Experimental Evolution Lectures,” folders 1 and 2.

<sup>309</sup> APS Davenport, Series II, Box 100, “A Summary of Progress in Experimental Evolution.” In his lectures and in a “lines of work” section of his application, his classes are similar, although in his lectures, he classified selection into its own category (whereas here selection studies, such as Weldon’s work, are included under “study of individual variation”). In his lectures he also included a heading for “control of pleomorphism” (stark changes in bacterial form), which he did not elaborate upon and appears nowhere else in his work as far as I can find. Note that my discussion that follows combines comments from his “Summary of Progress” along with his lecture notes.



Davenport's pluralistic treatment of evolution can be witnessed in his discussions of the effects of domestication and multi-generational captivity (2, 5) in addition to the inheritance of acquired characters and self-adjustment (which he would later reject) (3). Indeed, while he thought "results gained from rearing animals for a long time under changed conditions of life" were "surprisingly few," there was "plenty of experimental proof that climatic factors cause a change in the specific characters of the individuals acted upon." For example, in 1864, "Dorfmeiser found that chrysalids of the butterfly *Venessa*, normally destined to develop into the winter form ... might be forced to develop into the summer form ... or at least something approaching to it by heat." Other studies of *Lepidoptera* by Weismann and Fischer lasted only one to three generations, and were, according to Davenport, of limited value.<sup>310</sup> Biologists had discovered nutritional effects upon insect color, but the question remained "whether from such peculiarities in the course of years a new specific form could become established."<sup>311</sup> He noted the "pioneer" transplantation experiments of Bonnier, but again emphasized the neglect of carrying out the work across multiple generations.<sup>312</sup> In a section explicitly dedicated to "inheritance of acquired characters," he emphasized the attempts of Weismann and Galton to disprove neo-Lamarckism and Darwin's theory of pangenesis. A related theory, telegency, "or the alleged modification of offspring through some influence left on the mother by a previous sire" was a common belief among breeders, but biologists Romanes and Ewart had conducted experiments that indicated it was rare and not important in evolution. Davenport did not elaborate any further (and appears to have never investigated it).

Scientists using statistical methods had detected correlations between environmental fluctuations and populational variation, usually with the goal of detecting selection and adaptation (1). These studies included Allen's rule (the colder the climate the shorter an animals' limbs) and the previously discussed study by Weldon of Plymouth crabs. Additional work included biometrical studies of mollusk shells in relation to the stillness and density of water in Cold Spring Harbor by Davenport himself and Abigail

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<sup>310</sup> He also discusses this work, as noted above, in Experimental Evolution Lectures, folder 2.

<sup>311</sup> In an earlier draft, Davenport had included this work under the heading of "self-adjustment" or plasticity.

<sup>312</sup> Bonnier's transplantation work was the direct inspiration of Frederic Clements' method of experimental evolution.

Dimon.<sup>313</sup> Davenport also included the research of de Vries in this category for “combining experiment with measurement” to modify “the form of the distribution polygon.” An advantage of Davenport’s program was that he championed Mendelism while incorporating biometrical methods, a stance that shaped the Station’s activities during his tenure and American experimental evolution in general.

Davenport turned to natural selection, or “selective annihilation” (parallel to “selective mating”). He characterized selection as when “external agents” did not modify the germ plasm, but instead eliminated germ plasms that “produce somas ... unfitted to live” or “distinctly less fit to live than their fellows.” Furthermore, selection could act upon both “trivial variations” and “sports.” Not relegating selection to a minor role in evolution, Davenport wrote, “selection is a universal and necessary factor in ... determining the kind of germ plasm that shall survive in directing its movement.”<sup>314</sup> Davenport cited several selection studies, particularly the work of Bumpus, Crampton, and Weldon.<sup>315</sup>

Hugo de Vries’ mutation theory (4) and work on the evening primrose had launched a new interest in sports, enough for Davenport to classify it as a growing area of experimental study. As with other theories, the existence and importance of sports were primarily evidenced by the “undoubted fact that many domesticated and even some wild races seem to have started with such sports,” such as merino and Ancon sheep, as well as several plants. He wrote, “we have also the testimony of successful breeders of plants and

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<sup>313</sup> Abigail Camp Dimon, “Quantitative Study of the Effect of Environment upon the Forms of *Nassa Obsoleta* and *Nassa Trivittata* from Cold Spring Harbor, Long Island,” *Biometrika* 2, no. 1 (1902): 24–43.

<sup>314</sup> APS Davenport, Series I, Box 37, “Experimental Evolution Lectures” folder 2. This is a clear example of how natural selection was clearly accepted by many biologists; the question is whether it fit Darwinian interpretations.

<sup>315</sup> Bumpus’ work was to statistically analyze the morphological traits of 64 house sparrows that died during a severe winter storm in New England compared to 72 that had survived. He found several traits that correlated with survival and death, determining that the storm acted as what we would call today stabilizing selection. George M. Cook points out that while the work was used as an example of selection in the wild, Bumpus emphasized that its stabilizing effect was not creative. Davenport suggested however that this type of selection could split a species into two, “in some cases, at least, evolution seems to take place by small differences rather than by leaps, etc.” Hermon C. Bumpus, “The Elimination of the Unfit as Illustrated by the Introduced Sparrow, *Passer domesticus*,” in *Biological Lectures from the Marine Biological Laboratory at Wood’s Holl, Mass. 1898* (Boston: Ginn & Company, 1899), 209–26; George M. Cook, “Neo-Lamarckian Experimentalism in America: Origins and Consequences,” *The Quarterly Review of Biology* 74 (1999): 417–37.

animals that they get results quicker by hunting for sports among a large random produce than by the selection of individual variations.” As would soon become a prominent theme among biologists, “up to the present time no means has been discovered for getting any desired sport. ... Clearly a great step will have been gained when we shall know how to call forth at will any wished-for sport.” What interested Davenport, though, was the fate of a sport in the wild, “a crucial experiment.”

Studies on sports were intimately tied with experiments “on the nature of inheritance in normal [intra-species] crossing” and inter-species hybridization (6, 7). Here Davenport emphasized the research on blending and alternative inheritance by Mendel and his followers. (Note that Mendelism refers not only to heredity but to the transformative process of hybridization.) He wrote, “as Galton says, a peculiar interest attaches to alternative inheritance because of the aid that it must afford to the establishment of incipient races.” Not yet swept up by Mendelism, he also mentioned Karl Pearson’s demonstration that stature and skin color blended. He noted the extensive work and historical legacy of hybridization research, especially regarding its use to demarcate species. Now, he noted,

While many of the early hybridizers sought primarily to discover the laws of hybridizing (and of these Darwin is a notable example) the work of to-day is almost wholly in the hands of commercial horticulturalists or of government experiment stations. These too often look with disdain on the work of dabbling with the unknown for the sake of discovering general laws, instead of gaining some immediately practical result. Very recently, however, a new school has arisen from whom great things have already begun to appear.<sup>316</sup>

(8): Lastly, Davenport discussed “the effects of isolation” (8). He wrote, “a careful study of species in nature seems to prove that there is a close relation between the origin of species in nature and the isolation of parts of the old species. Yet there have been few experiments on isolation attempted.” In his lecture notes under the heading of “Isolation,” he quoted in full two brief notices by T. D. A. Cockerell in *Nature*. First, Cockerell communicated a report from a California local that the individuals of a group of goats stranded on an island looked identical, whereas its mainland relatives showed greater

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<sup>316</sup> This school included de Vries, Carl Correns, H. C. Webber, and Lucien Cuénot.

diversity. Second, Cockerell pointed to a recent monograph that described 134 distinct races of *Cerion* snails in the Bahamas, material he thought would be useful for the study of the possible effects of selection on specific differences.<sup>317</sup> Although Darwin discussed a natural experiment of two sheep colonies separated for fifty years becoming dissimilar, Davenport argued that “no experiment is more needed than that of keeping two carefully measured races in isolated but climatically similar regions for a long number of generations to observe the differences that crop out in them.”<sup>318</sup>

Curiously, the experiment he discussed at most length was Friedrich Hunger’s work with *Aspergillus niger*, black mold, perhaps because of how the work illustrated the theoretical and methodological importance of the environment. As Davenport emphasized, standardized environments were critical to experimental evolution and Hunger did so by using precisely controlled media and varying solution density with salt.<sup>319</sup> Among three lots of *Aspergillus* raised in denser solutions for 0-2 generations, Hunger found that descendants raised in a denser solution could thrive in even denser solutions, indicating adaptation, but did not thrive as well in the original control solution. From this experiment, along with a few others, Davenport concluded that modifications in response to density and temperature were inherited, whereas modifications in response to light, gravity, and use and disuse, were not.<sup>320</sup> The work also showed the difficulties inherent to experimental evolution, particularly in how to differentiate competing hypotheses, such as whether changed conditions shaped the soma and transmitted the changes to the germ, or shaped both simultaneously. Thus, for Davenport, the immediate result was a pluralistic view of evolution. He had written publicly that “the signs of the times indicate that we are about to enter upon a thorough, many-sided, inductive study of this great problem, and that there is a willingness to admit that evolution has advanced in many ways.”<sup>321</sup>

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<sup>317</sup> T. D. A. Cockerell, “The San Clemente Island Goat,” *Nature* 65, no. 1672 (1901): 31; T. D. A. Cockerell, “The Evolution of Snails in the Bahama Islands,” *Nature* 66, no. 1698 (1902): 56.

<sup>318</sup> APS Davenport, Series I, Box 37, “Experimental Evolution Lectures,” folder 2.

<sup>319</sup> The method was established by Léo Errera, “Hérédité d’un Caractère Acquis Chez Un Champignon Pluricellulaire,” *Bulletins de l’Académie Royale Des Sciences, Des Lettres et Des Beaux-Arts de Belgique* (1899): 81–102; Léo Errera, “Inheritance of Acquired Qualities,” *The American Naturalist* 33, no. 390 (1899): 522–23.

<sup>320</sup> APS Davenport, Series I, Box 37, “Experimental Evolution Lectures,” folder 2.

<sup>321</sup> Davenport, “Zoology of the Twentieth Century,” 318.

This history and classification influenced the directions Davenport thought a Station for Experimental Evolution should take. In another document, Davenport generalized the scientific concepts his Station would study: the shape of the “variation polygon” in different environments, the causes of variation, self-adjustment of an individual in a new environment, “the conditions under which sports may be induced or, perhaps, produced at will” and their fate in a natural environment, the “limits” and “different classes” of inheritance, and the role of hybridization in evolution.<sup>322</sup> In his “statement of eight experiments,” Davenport imagined a set of experimental studies that further illustrated his grandiose vision – but most of which never occurred. These were a genetic, biometric, and biogeographical study of the snail *Helix nemoralis* using 1,000 breeding pairs; a genetic study of endemic chinch bugs that display two distinct morphs (long wing and short wing); a study of direct environmental effects on the common pond snail *Limnaea*; a genetic study of a spider in which the males show two different morphs; a genetic study of a sporting Neapolitan goat (and possibly “polydactyl cats and abnormal rodents”); a general test of Mendel’s laws using guinea pigs, mice, and moths; a study of the effects of inbreeding and genetic isolation over eight or ten generations in lady-bird beetles and other species; and, an attempt to evolve marine animals such as the beach flea and the shore snail into terrestrial forms “by gradually acclimating them to dryer conditions.” The general method: “Experiments with the greatest attainable precision, under well controlled environmental conditions. Large numbers of individuals must be used and the characters of progeny and offspring are to be measured.”<sup>323</sup> All of this required money, personnel, infrastructure, and time.

### **“To Get Better Fruits”**

Accepting Davenport’s application, CIW decided to build the Station in Cold Spring Harbor on Long Island, New York, providing \$34,250 in funds to establish it. Although the location sacrificed the steady climate of a place like California, it was closer to a larger number of biologists and libraries — less than 30 miles from New York

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<sup>322</sup> “Some of the lines of work of a Station for the Experimental Study of Evolution,” n.d., APS Davenport, Series I, Box 100, “Dept. of Genetics - History” folder.

<sup>323</sup> “The [?] on Experimental Evolution which it is desired to start at the Cold Spring Station, and for which Assistance is Asked,” n.d., APS Davenport, Series I, Box 100, “Dept. of Genetics - History” folder.

City. Furthermore, Cold Spring Harbor offered a variety of habitats as well as a “free offer of about ten acres of land, with house and stable and horse shed.”<sup>324</sup> The land was leased from the Wawepex Society, which had also leased land to the Long Island Biological Association, adjacent to the Station. On June 11, 1904, a gathering of locals, journalists, administrators, and scientists, including Hugo de Vries, inaugurated the Station for Experimental Evolution.<sup>325</sup>

After Davenport introduced himself, John S. Billings, the chairman of CIW’s board of trustees addressed why they had decided to fund the Station.<sup>326</sup> Recognizing that applications may be slow to come, dedicating the funds to this project was still worthwhile because

the results of biological research have had a strong influence on philosophy and theology, and we can hardly even imagine what the outcome may be in sociology and political science. The problems of evolution and development through heredity involve the structure and functions of that part of the living organism which seems to be necessary for what we call mental action, from the lowest, dimmest forms of consciousness, through memory and will to the highest flights of art, philosophy, poetry, and religion.<sup>327</sup>

CIW had high hopes for the Station. While there is little mention of it in the Station’s first few years, it is no surprise that CIW, Davenport, and the Station would embrace eugenics as a form of applied science with its implications for “sociology and political science.” Clearly CIW thought the Station would produce results beyond the mere confirmation and refutation of evolutionary hypotheses such as the Mendelian laws of inheritance.

Davenport had requested de Vries to “formally open” the Station, as he was experimental evolution’s “God-father” and “the one person who has done most to stimulate the line of work which we are to pursue.”<sup>328</sup> Davenport introduced de Vries as the author *Die Mutationstheorie*, “a work destined to be the foundation stone of the rising science of experimental evolution.”<sup>329</sup> In his address entitled “The Aim of Experimental

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<sup>324</sup> CIW Yearbook, Vol. 3, 1904, p. 23.

<sup>325</sup> Other attendees included Frank Lillie, Henry E. Crampton, Daniel T. MacDougal, H. J. Bumpus, William Castle, and Nathaniel and Elizabeth Britton.

<sup>326</sup> For the sake of brevity, I will refer to the “Station for Experimental Evolution” as “the Station.”

<sup>327</sup> CIW Yearbook, Vol. 3, 1904, p. 38.

<sup>328</sup> Davenport to Hugo de Vries (1904/4/17) and Davenport to Hugo de Vries (1904/3/22), APS Davenport, Series I, Box 93, folder 1.

<sup>329</sup> CIW Yearbook, Vol. 3, 1904, p. 39.

Evolution,” de Vries declared

A bright prospect opens before us. ... Strenuous endeavors are proposed to wrest from nature secrets which not long ago seemed almost impregnable. The matter of the evolution of organic life on this earth, hitherto a subject of great admiration, admitting only of appreciative and comparative studies, is to be investigated to its very core. We are no longer content to look at it in a broad way, to enjoy the mighty display of harmony between all living beings and to sit down and wonder. *We want to have a share in the work of evolution, since we partake of the fruit. We want even to shape the work, in order to still get better fruits.*<sup>330</sup>

Emphasizing a Baconian approach to the study of evolution just as Davenport had, de Vries continued: “Evolution must become an experimental science. First it must be controlled and studied, afterwards conducted along selected lines, and finally shaped to the use of man.” For de Vries, “science is a mighty means of broadening our conceptions and our ideas, as well as our power to utilize the laws and materials of nature.”<sup>331</sup>

De Vries emphasized that experimentation would elucidate contemporary causes, not historical narratives. He said,

The process of the evolution of animals and plants has to be attacked by direct experiment. This evolution, however, has a long history, covering many millions of years. Its historical part, of course, is not accessible to experimental work. From its innermost nature it must be studied according to historical and comparative methods. In laboratory work we may simply pass it by.<sup>332</sup>

He also suggested that, due to the uniformity of the laws of nature across time, species may even be arising in the present (and that pre-cellular life may be detected in the oceans!).

De Vries then laid out two broad approaches to experimental evolution on both

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<sup>330</sup> Hugo de Vries, “The Aim of Experimental Evolution,” in CIW Yearbook, Vol. 3, 1904, p. 39. Emphasis added.

<sup>331</sup> de Vries, 39–40. For example, “We may hope some day to apply the physiological and activity of the rays of Röntgen and Curie to experimental morphology” (p. 43). Strangely, the example he provided was more experimental embryology (which Davenport had excluded from the Station’s program), not evolution. In a white peacock, if biologists could “seize upon the representative particles of the color and impede their development, perhaps we would succeed in reproducing the white variety at once and quite artificially.” De Vries also cited the embryological work of Engelmann, Johannsen, Overton, Wilson, Loeb, and Delage, specifically their contributions towards stimulating or inhibiting growth.

<sup>332</sup> de Vries, 44.

plants and animals: through biometry, “the direct study of variability,” and through experiment, a study of “the dependency of this variability on the outer conditions of life.”<sup>333</sup> While biologists conducted both styles of inquiry, de Vries concluded they were rarely if ever combined. He considered Davenport’s training in both schools as a unique strength for the Station.<sup>334</sup>

Defending the mutation theory and his method of discovering mutations, de Vries reiterated the further need to determine causes and this quest’s association with power. It was the knowledge of causes that would “enable us to take the whole guidance of it [mutation] into our own hands.” As difficult as this was, de Vries was confident that “this aim lies within the possibilities of the first series of years.” Regarding mutations, he suggested that

exact methods of working, severe isolation of the single individuals, artificial fecundation with complete exclusion of the visits of insects, and above all the great principle of individual seed-saving and seed-sowing, have to be the guides. Following the lines which are indicated by these prescriptions, gradually a power will be developed which will first enable us to increase the number of mutating seeds and afterwards to widen the range of mutability. New and unexpected species will then arise, and methods will be discovered which might be applied to garden plants and vegetables, and perhaps even to agricultural crops, in order to induce them to yield still more useful novelties.<sup>335</sup>

In closing his address, de Vries lamented that the Station was “the most dreadful competition that I could have,” to which “I have to yield my much beloved child,” but “it is the interest of the child itself which commands me.” And thus, its godfather blessed the opening of the Station for Experimental Evolution.

Davenport reiterated the goals of the Station announced by de Vries and Billings through his annual reports to CIW. In 1906, he reminded the leaders of CIW that the station’s “present aims” were to understand biological evolution in order to “improve the

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<sup>333</sup> de Vries, 45.

<sup>334</sup> “Fluctuating variability, however, has been the chief line of study [via biometry] for Mr. Davenport, and he would be a bold man who would try to show the way where such a guide is at hand” (p. 46).

<sup>335</sup> de Vries, “The Aim of Experimental Evolution,” 48. Here he cited the plant breeder Korshinsky. It is also worth noting that de Vries later published a book dedicated to plant breeding. Hugo DeVries, *Plant-Breeding: Comments on the Experiments of Nilsson and Burbank*, by Hugo de Vries. (Open Court Pub., 1907). Note de Vries’ focus on plants in contrast to Davenport’s emphasis on animals.



human race,” as well as understand “how organisms may be best modified to meet our requirements of beauty, food, materials, and power.” He reported the following year, claiming that its purpose was to ask, “How may the course of the stream of germ plasm that has come down to us from remote ages be controlled in its onward course?”<sup>336</sup> In 1908, he wrote,

Certain portions of that unending stream of reproductive matter which has come down to us from the time when life began on earth and by changes in which all evolution has taken place are now under our careful observation and to a large extent under our control. It is the business of the Department of Experimental Evolution to study the behavior of this germ-plasm and to note its reaction to the conditions we impose.<sup>337</sup>

Direct application was not the immediate goal of the Station. CIW sought to avoid replicating the work of the fifty-six American agricultural experiment stations as well as the federal bureaus of Animal Industry and Plant Industry, institutions too burdened with practical work to study potential new laws and principles. Davenport wrote,

We could easily produce new and valuable races. We could do all these things with certainty by the application of well-known and constantly employed principles. But we prefer to risk certain results for the uncertainty of attaining new principles. ... We propose to leave the question of application to others, bending our whole energy to our main work – the discovery of general principles or laws.<sup>338</sup>

Thus, the Station undertook basic research to inform applied science. The need to do so was shown by history: Mendel, unconcerned with “making plants more beautiful or useful,” discovered a principle of “inestimable value to breeders” that went “overlooked by the practical breeder, and through thirty-five years of practical work was never rediscovered by the thousands of breeders or the scores of experiment stations.”<sup>339</sup> This reasoning attested to the notion that biologists needed to move beyond Darwin’s reliance on breeders to work out the deeper method of evolution.

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<sup>336</sup> CIW Yearbook, Vol. 6, 1907, p. 76; Vol. 5, 1906, p. 92.

<sup>337</sup> CIW Yearbook, Vol. 7, 1908, p. 86.

<sup>338</sup> CIW Yearbook, Vol. 5, 1906, p. 93. This is slightly exaggerated; the next chapter shows that East and Pearl combined practical work with natural science, but experimental evolution was not the priority of any station.

<sup>339</sup> CIW Yearbook, Vol. 5, 1906, p. 93. Note that Mendel’s work was built upon prior research on ornamental plant color, but it was not his immediate goal.

Furthermore, direct application was limited by the nature of most biological organisms. As Davenport wrote, “Nature is in no hurry, and for most animals and plants it takes a year to make a single onward step.”<sup>340</sup> CIW’s president, Robert S. Woodward, recognized that experimental evolution differed from other experimental sciences, writing that “a decade is the smallest convenient time unit for measuring the progress” of work at the Station.<sup>341</sup>

Alongside the Station for Experimental Evolution, CIW established the Desert Botanical Laboratory in Tuscon, Arizona under the auspice of a Department of Botanical Research. Woodward reported,

A considerable knowledge of biology, of plant, insect, and animal life is, indeed, now essential to successful economic husbandry; but although tradition has furnished a large aggregate of useful inductions for the needs of agriculture and horticulture, it is only in recent decades, dating substantially from the advent of Darwin's great work, that such inductions have begun to rise to the level of coordinated knowledge.

The laboratory was directed by Daniel Trembly MacDougal, much of his work also directed towards experimental evolution. In fact, he was an early disciple of Hugo de Vries and a champion of the mutation theory.<sup>342</sup> That his research was directed towards inducing mutations demonstrates that CIW dedicated serious resources to the emerging program.

### **The Station: 1904-1909**

The early years of the Station were dedicated to preparation. Hired to the station were four resident scientists and four “helpers.” In addition to Davenport, the resident staff included geneticist and botanist George H. Shull, entomologist Frank E. Lutz, and cytologist and secretary Anne M. Lutz (unrelated). (I ignore Shull’s maize work in this chapter, because it is central to Chapter 4, but it also happens at the Station during this period). Roswell Johnson, whose application to CIW I quoted above, joined them a short

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<sup>340</sup> CIW Yearbook, Vol. 6, 1907, p. 76.

<sup>341</sup> CIW Yearbook, Vol. 5, 1906, p. 23.

<sup>342</sup> MacDougal’s research was expansive, similar to Davenport’s early career before the Station. Sharon Kingsland’s article on MacDougal, “The Battling Botanist,” is one of the few histories of science dedicated entirely to experimental evolution (*Isis* 82, no. 3 (1991): 479–509).

time later. The helpers included a part-time librarian, a mechanic, an animal caretaker and janitor, and a gardener. A series of associates received funding through the Department of Experimental Biology or collaborated with one of the resident staff. These included Nathaniel Britton, William Castle, Henry Crampton, E. L. Mark, Daniel MacDougal, William J. Moenkhaus, William Tower, and E. B. Wilson, who all worked on some aspect of experimental evolution, whether it was mutation studies, hybrid breeding, selection experiments, or cytological investigations. There were also correspondents, including Bateson, Correns, Cuénot, Hurst, Tschermak, and C. O. Whitman. The Station for Experimental Evolution was not only a place, but also the center of a growing network of experimental biologists in the United States funded by CIW.<sup>343</sup>

The establishment of animal and plant colonies required considerable effort. In his first reports, Davenport divided the work by “material” (species) rather than topic because “especially among animals, each kind of material offers special difficulties in rearing and breeding that have to be mastered before further progress can be made,” and due to slow reproduction, such mastery could take years to accomplish.<sup>344</sup> As the Station opened, Davenport was breeding “cows, sheep, goats, cats, poultry, and canary birds,” planning to test characters for Mendelian ratios, as well as experimenting with “wild species of crustacea and mollusca.”<sup>345</sup> The entomologists determined which species were useful and how to raise them, in terms of workable crosses and the unique conditions of captivity required by each species.<sup>346</sup> Frank Lutz’s goal was to investigate the Mendelism of wing lengths in addition to assortative mating. Johnson reported the difficulties in determining the best species of plant-lice (food) as well as temperatures for his lady-beetles, testing, as Davenport had emphasized, whether “laboratory conditions would in themselves produce modifications,” finding only one instance.<sup>347</sup> Plants required less maintenance, but their mating systems were “more difficult to control.” They were also prone to “weeds, ... parasitic plants and animals,” and meteorological conditions, so, an irrigation system was constructed to protect plants from drought. Their environmental

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<sup>343</sup> CIW Yearbook, Vol. 3, 1904, pp. 28-29.

<sup>344</sup> CIW Yearbook, Vol. 4, 1905, p. 87.

<sup>345</sup> CIW Yearbook, Vol. 3, 1904, p. 29; CIW Yearbook, Vol. 4, 1905, pp. 92-94.

<sup>346</sup> CIW Yearbook, Vol. 4, 1905, p. 89.

<sup>347</sup> CIW Yearbook, Vol. 5, 1906, pp. 102-103.

sensitivity meant that Shull had to find plants “which will tolerate the production of adaptive structural modifications.” He began preparing an abandoned garden plot, but in the meantime collaborated with MacDougal at the New York Botanical Garden to grow seeds given to the Station by Hugo de Vries, including (but not limited to) *O.*

*lamarckiana*. He also grew crops as feed and to sell, saving some that showed potential hereditary variations.<sup>348</sup> Immediately the Station was proving the argument that a well-funded institution was required to make headway in experimental evolution.

This argument was further proved by the physical infrastructure. As Kohler notes, “it was not a biological farm, exactly, but more biodiverse and integrated with its natural surroundings than any laboratory, then or now.”<sup>349</sup> When the Station opened in 1904, it consisted of only one research building, 60 feet by 35 feet, two stories high with a basement. On the ground floor were rooms for breeding animals and another to house aquatic animals, along with smaller rooms for food preparation and work. Above was a series of five research rooms, a secretary’s office, a library that could hold 1,000 books, and a room with a glass roof for plants, birds, and insects. The attic could hold a further 7,000 books. The basement had rooms for food and tool storage, heating facilities, a photographic dark room, a “low temperature room,” and an artificial “dark room” for “cave studies.” The station was electrified for both power and light and heated by steam. For the following year, Davenport planned to build a greenhouse, a wire roof for the experimental garden, and outdoor fishponds. (Given the severity of accidents in ruining experimental studies of evolution, the building was fireproof — a fortuitous decision as a fire that broke out in the middle of a night in 1906 “due to the carelessness of a workman ... was confined to the room in which it started.”)<sup>350</sup> But within one year, the Station was already at its infrastructural limits, thus, building a poultry-house, brooder-house, the green-house, and fourteen small chicken-houses. In following yearbooks, Davenport reported the construction of a vivarium (for insects), a birdhouse (for genetic studies of canaries), and additional small green-houses to grow food for the insects and birds. The Station built forty portable “colony houses” in addition to fifty new breeding

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<sup>348</sup> CIW Yearbook, Vol. 4, 1905, p. 88; Vol. 3, 1904, p. 30.

<sup>349</sup> Robert Kohler, *Landscapes and Labscapes* (Chicago: The University of Chicago Press, 2002), 48.

<sup>350</sup> CIW Yearbook, Vol. 3, 1904, pp. 24-27; Vol. 5, 1906, p. 97.

pens. They also hired more workers, including a poultryman. The work of the Station was proving biologists' realization that experimental evolution required permanent infrastructure and significant capital funds, especially given Davenport's wide-ranging vision.<sup>351</sup>

Davenport remarked, "it is a feature of experimental work in biology that it tends to increase geometrically." In 1906, Shull reported that 46 plant species had been raised and measured, composed of 291 pedigrees of 29,077 individuals. Lutz had measured 2,000 pedigreed individuals of *Gryllus* (field crickets). Separately from the Station proper, Moenkhaus and Castle had themselves raised over 10,000 flies and 3,000 rodents, respectively. This was in addition to the dozens of strains of poultry, cage-birds, and mammals.<sup>352</sup> To track and control the rapidly growing numbers of experimental organisms, Station researchers implemented pedigrees. Shull developed a card catalogue to track pedigreed lineages and data regarding variability and heritability. Davenport pointed out that pedigrees not only controlled for confounding variables, but existed for the sake of control. He wrote they had started

a certain number of strains with the intention of controlling their onward progress, first by controlling all matings, and, secondly, by controlling or at least observing the environmental conditions.<sup>353</sup>

Significantly in 1908 Davenport and his wife, zoologist Gertrude Davenport, extended the Station's pedigree-keeping to human eye and hair color, signaling the introduction of eugenics based on Mendelism. Davenport claimed that the Station had accumulated "a lot of pedigree data—much of it quantitative—the like of which exists, I venture to think, nowhere else in the world."<sup>354</sup> While not experimental in themselves, careful pedigrees "have much the value of experimental data" that could enable predictions.<sup>355</sup> (Note that pedigrees had emerged from within the experimental context of breeding, in general.) This was evidenced by his own work in the inheritance of chicken

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<sup>351</sup> CIW Yearbook, Vol. 4, 1905, p. 95; Vol. 5, p. 97; Vol. 6, 1907, p. 83.

<sup>352</sup> CIW Yearbook, Vol. 4, 1905, p. 96; Vol. 5, 1906, pp. 97-98; Vol. 7, 1908, p. 91; Vol. 5, 1906, pp. 105, 243.

<sup>353</sup> CIW Yearbook, Vol. 6, 1907, p. 76.

<sup>354</sup> CIW Yearbook, Vol. 7, 1908, p. 89.

<sup>355</sup> CIW Yearbook, Vol. 10, 1911, p. 79; Vol. 7, 1908.

color, which even as a result of multiple factors could be expressed in “simple formulae ... by which the proportions of any color in a given hybrid mating can be predicted.”<sup>356</sup> This combination of natural history (pedigrees) and experimentalism had brought Davenport to eugenics, a subject not explicitly discussed in his applications or mission statements, but would become one of the Station’s most infamous contributions to early twentieth-century biology.

The work increased geometrically not only in population sizes, but in lines of investigation. Despite employing only four or five scientists, their research included assessing the mutation and pure line theories, de Vries’ primroses, the effects of inbreeding, the breadth of Mendelian inheritance, the breeding methods of Luther Burbank, and whether or not “new, inheritable characteristics” “can be induced of a desired sort” “so that evolution can be directed at will.”<sup>357</sup> The still somewhat practical bent of the Station was evident in the organisms used for study: while *Drosophila* played some role and biologists elsewhere made use of *Paramecia* and hydra, many of the species at the Station were crops or livestock. The bias towards domesticated species is indicated by Davenport’s research on canaries: he used a semi-domesticated bird to refute the claim that Mendel’s laws applied only to domesticated varieties.<sup>358</sup> The canary also reveals that domesticated animals and plants were so common in part because such organisms are easier to handle given their co-evolution with and recently directed evolution by humans, a transition from wild species to model organisms.

The Station’s collective reports reveal the confusion and contradictions that permeated evolutionary science at the time during the so-called “eclipse of Darwinism.” Davenport himself wrote in support of Mendelism, unit characters, and the mutation theory; however, he remained open to Castle’s theory of genetic contamination.<sup>359</sup> Associate William Tower, on the other hand, emphasized continuity and the non-

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<sup>356</sup> CIW Yearbook, Vol. 9, 1910, p. 77.

<sup>357</sup> CIW Yearbook, Vol. 5, 1906, pp. 94-95. During this time, Shull was appointed to a project to study and hopefully systematize the breeding methods of Luther Burbank. CIW allocated \$10,000 per year between 1904 and 1909 for the project. The project was deemed unsuccessful, partially due to personality conflicts. See Bentley Glass, “The Strange Encounter of Luther Burbank and George Harrison Shull,” *Proceedings of the APS* 124 (1980): 133–53.

<sup>358</sup> Davenport, *Inheritance in Canaries* (Washington, D. C.: CIW, vol. 95, 1908).

<sup>359</sup> CIW Yearbook, Vol. 5, 1906, p. 94. Genetic contamination is a major topic of the following two chapters.

randomness of variation, dismissing mutations. Frank Lutz, carrying out similar work to Tower on insects, had found Mendelian inheritance in color patterns.<sup>360</sup> Roswell Johnson followed Lutz in concluding that species and varieties of *Hippodamia* (ladybeetles) expressed Mendelian inheritance and arose by mutations, “intergrades in nature and in the laboratory [being] very rare.” But he agreed with Tower that mutations were orthogenetic (contra de Vries), believing that “polyphyletic origins of varieties and species must be far more common than generally supposed.”<sup>361</sup> Both Tower and Johnson rejected selection as important, although William Castle, a CIW-funded associate at Harvard, began to argue for selection’s power and utility while challenging common Mendelian notions such as its use for explaining blending inheritance; Davenport at this time accepted Castle’s skepticism.<sup>362</sup> Johnson declared instead that “evolution is very active” through mutation and environmental stimulus.<sup>363</sup> Henry Crampton, another CIW-funded correspondent, thought that variation in snails (*Partula*) on the Society Islands were mutations that were *not* environmentally caused.<sup>364</sup> Davenport rejected the inheritance of acquired characters but remained open to its possibility. He did write that “it can not be doubted” that some environmental stimuli triggered mutations, as Bonnier, Lutz, Tower, Johnson, and others had found. Furthermore, their work showed that variations occurred in a “definite direction,” even in nature.<sup>365</sup> Meanwhile, Shull (with Edward East) was developing the mutation theory, challenging Darwin’s ideas about inbreeding, and investigating how variation, heredity, and selection interacted. Out of these messy results, the strongest statement Davenport could muster was that the Station had “confirm[ed] the fundamental importance of Mendel’s law.” Particularly, they had “silenced the objection that [Mendelism] related only to ‘artificial’ varieties and proved that they hold equally for

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<sup>360</sup> CIW Yearbook, Vol. 5, 1906, pp. 250, 100.

<sup>361</sup> CIW Yearbook, Vol. 6, 1907, pp. 79-80. This meant a species could arise multiple times from the same stock via the same mutations. Johnson was not comfortable calling this phenomenon “orthogenesis,” using “determinate variation” instead. Johnson, *Determinate Evolution in the Color-Pattern of the Lady-Beetles* (CIW, vol. 122, 1910).

<sup>362</sup> Davenport, “Recent Advances in the Theory of Breeding,” *Proceedings of the American Breeders’ Association* 3 (1907), 133.

<sup>363</sup> CIW Yearbook, Vol. 6, 1907, p. 81.

<sup>364</sup> CIW Yearbook, Vol. 7, 1908, p. 244. For more on Crampton, see Robert E. Kohler, *Landscapes and Labscapes: Exploring the Lab-Field Border in Biology* (Chicago: University of Chicago Press, 2002).

<sup>365</sup> CIW Yearbook, Vol. 7, 1908, pp. 87-88; Vol. 8, 1909, p. 88.

species in nature.”<sup>366</sup> This affirmed Davenport’s goal of discovering and working out laws of nature, as opposed to producing new horticultural and agricultural varieties, while also demonstrating that evolutionary science required significant investments to work out even modest conclusions.

As for taking control of evolution, the Station had made limited progress. In his five-year review, Davenport expressed uncertainty regarding the “modification of characteristics”:

By changed environmental conditions characteristics may, of course, be changed and the modifications, though usually somatic only, are sometimes transmissible (Tower). By selective breeding, characteristics may be modified, increased, or diminished, and there is evidence that such modifications are sometimes inherited. Thus Castle has shown that the extent of the pigmented area in rats may be varied in an inheritable fashion by selection of slight variations and, beginning with a scarcely recognizable trace of syndactylism, I have succeeded in getting very exaggerated forms of this condition. On the other hand attempts, in other cases, to increase or diminish characteristics (i.e., certain color-characters) by selection have not yet met with success. This whole subject of the modifiability (and particularly the inheritable modifiability) of characters deserves thorough investigation.<sup>367</sup>

De Vries had suggested that the scientific control of evolution (or at least, mutations) “lie within the possibilities of the first series of years,” but Davenport admitted this was not the case. He foresaw the dilemma as the “crux of the controversy between the Darwinian ‘selectionists’ and the De Vriesian mutationists,” a debate rooted in both theory and practice funded by CIW. All was well, though, because this is what CIW had expected.

Indeed, CIW kept the money flowing: after startup costs of \$70,000, CIW increased its annual funding of the Station’s research from \$12,000 in 1905 to \$29,000 in 1909. Capital costs, including land, construction, and maintenance, increased from \$23,201.81 to \$46,005.86, for a total of \$75,005.86 annually. Given the limits of scientific funding for the biological sciences in the early twentieth century, this was an astonishing amount. In fact, the amount of money, or more importantly, the *perception* that the Station was drowning in funds, proved to be somewhat of an issue: Woodward

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<sup>366</sup> CIW Yearbook, Vol. 7, 1908, p. 90; Vol. 8, 1909, p. 87.

<sup>367</sup> CIW Yearbook, Vol. 8, 1909, pp. 87-88.



complained that “our attempts at cooperation” with others “have in most cases led to difficulties, arising from an exaggerated estimate of the Institution’s capabilities.”<sup>368</sup>

The time required to conduct substantial work in experimental evolution apparently contradicted the professional careers of its resident scientists. In 1909, Frank Lutz resigned from the Station to take a position at the American Museum of Natural History. Roswell Johnson also resigned, finding a position at Pittsburgh and became an influential advocate of eugenics. To replace them, Davenport hired zoologist Arthur Banta, to work in the artificial cave, and Ross Gortner, a biochemist.<sup>369</sup> By 1920 only Davenport remained of the original scientific staff; in general, only the directors of the Station (i.e., Blakeslee, Demerec) spent more than a decade working at the Station.

The work of the Cold Spring Harbor station featured in several newspapers in its first years. The *New York American* wrote in 1910:

‘Freaks’ Are Bred to Get New Knowledge of Heredity.

Combless Poultry, One-Footed, Wingless and Tailless Birds Successfully Raised.

“To Aid Human Affairs”

Experimental Evolution Station Hopes to Indicate Characteristics of Unborn.<sup>370</sup>

The article functioned as a five-year update, acknowledging that the nature of the station’s work meant that “five years more will probably be employed in experiment and observation” before the Station would publicly reveal its results. Davenport told the newspaper that several characteristics in poultry had arisen *de novo* and were permanently inherited. The article focused not only on domesticated breeds, but also on Banta’s study “on the modifications which cave breeding produces in a species” and that “Tower has found he can breed a new Colorado potato beetle in high temperature and dry air in which the germ-plasm produces less pigment.”<sup>371</sup> It also mentioned the biochemical and cytological work of Gortner and Anne Lutz. The article also noticed the Station’s interest in eugenics, about which Davenport told them:

We are co-operating with the Committee of Eugenics in gathering data concerning the

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<sup>368</sup> Woodward to Davenport (1910/8/24), APS Davenport, “Woodward, R. S. 1910 Folder 2, May - August.”

<sup>369</sup> CIW Yearbook, Vol. 8, 1909, p. 89.

<sup>370</sup> “‘Freaks Are Bred to Get New Knowledge of Heredity,” *New York American* (1910/7/25), APS Davenport, Series I, Box 100, “Station for Experimental Evolution - History” folder.

<sup>371</sup> Davenport had described Tower’s research as having “tried, with much success, to control the origin of new characteristics in the Colorado potato-beetle and its allies.” CIW Yearbook, Vol. 8, 1909, p. 85.

transmission of human characteristics. ... Although not strictly within the scope of experimental work, the necessity of applying the new knowledge of heredity to human affairs is too important to be overlooked. Expectation is that it will be possible, in the case of the marriage of two individuals, even differing in characteristic, to state how the characteristic will be distributed among the children.<sup>372</sup>

### **The Station: 1910-1920**

Over the next decade, the Station's personnel, infrastructure, and projects continued to expand. By 1916, the Station employed about 20 staff, including seven resident scientists and several women (which grew temporarily during the military draft).<sup>373</sup> As the Station grew, so did the number and diversity of research projects, making the history difficult to summarize. As Davenport admitted in his 1923-1924 report, a "friendly criticism" of the Station was that "its investigations are somewhat diffuse and not concentrated sufficiently upon a single point."<sup>374</sup>

The fluidity of what constituted experimental evolution is perhaps best seen in the ever-shifting categories under which Davenport listed research projects in his annual reports. They also show that much of the work conducted by the Station was not directly *experimental evolution* — only three of the listed seven "principal developments" in 1911 were such: the publication of Frank Lutz's research on *Drosophila* (in which he "secured variations in the wing venation unlike anything known in nature" and showed that these were not lost by disuse), the end of Shull's study of Burbank, and the refutation of neo-Lamarckism. These three contrast with the establishment of the Eugenics Record Office, the discovery of how epilepsy is inherited in humans, the publication of James Arthur Harris' biometrical studies on plants, and Gortner's discovery of two types of melanin.<sup>375</sup> What CIW President Woodward considered the Station's most promising investigations also showed this ambiguity: Shull's study of "the effects of self-fertilization in maize" over time (Chapter 4) and the heredity of epilepsy in humans.<sup>376</sup> The following year, the

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<sup>372</sup> "Freaks Are Bred to Get New Knowledge of Heredity," *New York American* (1910/7/25).

<sup>373</sup> CIW Yearbook, Vol. 13, 1914, pp. 20-21; CIW Yearbook, Vol. 17, 1918, p. 104. In 1916, the Station had seven resident investigators: Davenport, Harris, Banta, Riddle, MacDowell (of the Castle lab), Metz, and Blakeslee. CIW Yearbook, Vol. 15, 1916, pp. 120-122.

<sup>374</sup> CIW Yearbook, Vol. 23, 1923-1924, p. 23.

<sup>375</sup> CIW Yearbook, Vol. 10, 1911, p. 78.

<sup>376</sup> CIW Yearbook, Vol. 10, 1911, p. 20.

Station's work had been conducted "chiefly along the lines of studies in cytology, in the chemistry of pigmentation, in the factors of mutation, and in the problems of human heredity."<sup>377</sup> 1914's reported accomplishments included the inheritance of depression, sex-limited inheritance of "nomadism" and alcoholism, polygenic inheritance, "experimental evidence ... of the selective nature of elimination" in plants, and "the evolution of the chromosomal complex."<sup>378</sup> The blend of experimental evolution, genetics, and eugenics along with cytology, biochemistry, and biometry continued throughout Davenport's tenure. The complex mix of evolutionary theories that characterized the Station's first years had given way to a more general biology centered around genetics. This reflected the consolidation among experimental evolutionists around the theories of de Vries, Johannsen, and Mendel against Lamarck, Eimer, Nageli, Henslow, and Delage.

Thus, Davenport did see theoretical progress made in the "methods of evolution" over the past decade through work which the Station had taken part in. He emphasized the discoveries that: 1) characters are independent of each other and their genetic "determiners" are not "bound together"; 2) genetic discontinuity passes into continuity with multiple factors and small mutations; 3) selection is optimized by selecting the "most favorable blood, race, strain or pure line (biotype, Johannsen)" rather than individual somas (which remains useful if necessary); 4) Mendelism and mutationism solved species formation by eliminating swamping as a problem; and 5) mutations occur independently from somatic changes but conditions may effect the germ plasm. He admitted that experimental evolution's contribution to the question of adaptation "has not been great," but that "on the whole, I think it may be fairly said that experimental work supports the principle of selective elimination but finds many characters that are wholly neutral."<sup>379</sup>

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<sup>377</sup> CIW Yearbook, Vol. 11, 1912, p. 18.

<sup>378</sup> CIW Yearbook, Vol. 13, 1914, p. 116. "Selective elimination"

<sup>379</sup> Davenport, "Light Thrown by the Experimental Study of Heredity Upon the Factors and Methods of Evolution." *The American Naturalist* 46, no. 543 (1912): 129–38. His elaboration on selection: In so far as not the soma but the germ-plasm is the proper basis of selection it is clear that the favorable biotype is what we should seek for to make most rapid advance. By this means Pearl has increased the fecundity of his poultry; thus, probably Castle has extended step by step the color pattern of rats; thus poultry fanciers have improved the color pattern of Barred Plymouth Rocks; thus I have gained a syndactyl race of fowl" (p. 133).

The possibility of controlling evolution remained an open question. In 1910 Davenport reported the quest to “induce at will a wholly new characteristic by experimental methods” remained unfulfilled, but by sheer numbers — 17,000 poultry, for example — new strains could appear.<sup>380</sup> Several years later, Davenport declared that “no student of evolution by experimental methods can doubt the importance of mutations,” but they remained outside of human control, limiting their investigation.<sup>381</sup> Mendelism explained how humans could “combine determiners at will” to “make new and improved breeds,” but this was the original point of Mendel’s work anyway.<sup>382</sup>

Davenport continued to raise large numbers of domesticated animals, assessing whether variations followed Mendelian laws and whether they functioned as mutations.<sup>383</sup> Davenport briefly collaborated with the New Hampshire Agricultural Experiment Station to improve sheep by “modern methods,” including Mendelian crossing and progeny-based selection.<sup>384</sup> The extensive use of pedigrees in this work was rather similar to eugenics pedigrees, one of the implicit ways that Davenport linked experimental evolution and eugenics.

Genetics had become the focus of the Station’s research. To display to CIW’s trustees the payoff of funding the Station, Davenport addressed them on “The New Principles of Heredity.”<sup>385</sup> While Davenport claimed in 1909 that the Station’s major achievement to be the confirmation of Mendel’s laws of inheritance in a diverse array of species, questions remained; “the subject ... [was] by no means ... exhausted.” Shull, Lutz, and Johnson reported “irregular” dominance, for example. The Station followed up the discovery of chromosomal mechanics, which included Anne Lutz’s study of *Oenothera* chromosomes, which produced “the suggestion ... that ‘mutation’ is always induced by some irregularity in chromosomal division.” While Anne Lutz soon departed

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<sup>380</sup> CIW Yearbook, Vol. 9, 1910, p. 75.

<sup>381</sup> CIW Yearbook, Vol. 12, 1913, pp. 102-103.

<sup>382</sup> CIW Yearbook, Vol. 12, 1913, p. 106.

<sup>383</sup> CIW Yearbook, Vol. 13, 1914, p. 117.

<sup>384</sup> CIW Yearbook, Vol. 14, 1915, p. 144; Vol. 16, 1917, p. 129. It was published as E. G. Ritzman and Davenport, “Family Performance as a Basis of Selection in Sheep,” *Journal of Agricultural Research* 10 (1917): 93-97. For some reason, Davenport recapitulated Bakewell.

<sup>385</sup> Davenport to Woodward (1910/9/17) and Woodward to Davenport (1910/9/23), APS Davenport, “Woodward, R. S. 1910 Sept. - December.” Davenport proposed appending “and Human Progress” to the title, but Woodward advised against it, worried the Trustees would get ahead of themselves in perceived applications.

following a dispute with Davenport, this project was a consistent part of the Station's work for over the next two decades led by Charles Metz and Albert Blakeslee.<sup>386</sup> Another sign of the Station's increasing focus on genetics was CIW's grants to the Morgan lab starting in 1915.<sup>387</sup>

This increased focus on genetics did worry Davenport, at least temporarily. In a memo to Woodward, Davenport admitted that "since its beginning this Station [for Experimental Evolution] has been chiefly engaged in studying the laws of inheritance... It has become plainer that there are other fields to be worked in the subject of experimental evolution which we have hitherto largely neglected." Davenport attributed this neglect to a "realization that the new lines of investigation would require a new and more expansive kind of equipment than that which we have possessed." Eugenics, or human heredity, had been funded by the railroad heiress Mary Harriman through the Eugenics Record Office, but other research programs required new capital and equipment. One new line of work included the effects of light upon pigmentation. The desire to control the production of mutations and to increase variability by changing the environment of the germ plasm," apparently required a new building of laboratories and animal shelters. Following the work of MacDougal and William Tower, in which the "application of ... agents" such as temperature and moisture could effect morphological and hereditary changes, Davenport sought to construct two rooms dedicated to either constant high or low temperatures.<sup>388</sup> He also proposed a project on the "surgical interference with the germ cells" as another method of inducing mutations. Sheep, useful for "determination of sex characters," and Whitman's pigeons, to which Oscar Riddle

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<sup>386</sup> CIW Yearbook, Vol. 9, 1910, p. 76; Vol. 11, 1912, p. 83. Whether mutation was genic or chromosomal was a major question addressed by the Station and experimental evolutionists; see Campos, *Radium and the Secret of Life*. For more on Lutz, see Marsha L. Richmond, "Women in Mutation Studies: The Role of Gender in the Methods, Practices, and Results of Early Twentieth-Century Genetics," in *Making Mutations: Objects, Practices, Contexts*, ed. Luis Campos and Alexander von Schwerin (Max Planck Institute for the History of Science, 2010), 11–48.

<sup>387</sup> Robert Kohler, *Lords of the Fly* (Chicago: University of Chicago Press, 1994), 106.

<sup>388</sup> Reporting on research concerning the "relation of physico-chemical properties of vegetable sap to environmental factors" (in collaboration with the Desert Lab), Harris highlighted the importance of understanding in full an organism's context: "Any attempt to influence the germ-plasm of species as a means of controlling evolutionary phenomena should, if it is to throw light upon the problem of the methods by which evolution has taken place in nature, be made by means of factors which are of fundamental biological importance in nature. Such factors are light, temperature, and moisture" (CIW Yearbook, Vol. 14, 1915, p. 146).

would dedicate several years, would be given more space. (Davenport even estimated the energy costs for this requested infrastructure.)<sup>389</sup> While he desired the Station to dedicate more resources to *inducing* these changes, Davenport did not mention natural selection or other relevant evolutionary mechanisms in the memo, despite some of his staff's active investigation of the subject.

Ten years following the Station's inauguration, Davenport reported that "the problem of variation ... still remains unanalyzed" and "finally, we have made a beginning on the task of inducing variations at will."<sup>390</sup> Under this heading, work included a search for mutations around Cold Spring Harbor, "periodicity in abnormality in the passion flower," "chemical and morphological differences in the sap of crape myrtle," "modification of the germ-plasm by alcohol" (in rats), and the use of a centrifuge to induce developmental changes in amphibian eggs.<sup>391</sup> Oscar Riddle apparently found a method to "force" pigmentation in albino doves and Banta reared a cave amphipod in daylight, suggesting the role of light in producing pigment.<sup>392</sup> Yet the "experimental modification of the germ-plasm" remained "the loftiest aim of the experimental evolutionist" but "has been so rarely achieved that all reported successes in this direction are received with critical skepticism."<sup>393</sup>

Research that blended experimental evolution with "immediate sociological importance" was G. C. Bassett's project, conducted under the direction of behaviorist John B. Watson, to produce genetic and mental changes in rats via alcoholic vapors.<sup>394</sup> Specifically, the work touched on whether "in man, alcoholism in the parents results in their children having less than normal mentality." What made this project odd among the Station's research projects is that it had no purpose of *improvement*. Davenport saw parallels with inbreeding in maize, leading to a proposal to use inbreeding and selection in rats to produce a "strain of rats of inferior intelligence," then use hybridization to test

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<sup>389</sup> Davenport to Woodward, n.d., "Woodward, R. S. 1912 Folder 2, Oct. - December."

<sup>390</sup> CIW Yearbook, Vol. 13, 1914, p. 120.

<sup>391</sup> CIW Yearbook, Vol. 13, 1914, pp. 120-122. Davenport suggested the speed at which changes occur is a "limit [that] serves, in a way, to measure the relative strength of hereditary and environmental forces in the given case of development." CIW Yearbook, Vol. 13, 1914, pp. 120-122.

<sup>392</sup> CIW Yearbook, Vol. 16, 1917, pp. 129-130.

<sup>393</sup> CIW Yearbook, Vol. 14, 1915, p. 131.

<sup>394</sup> Several years later, the project passed into the hands of resident scientist E. C. MacDowell, a former Castle student.

its inheritance.<sup>395</sup> This is one of the few explicit links between eugenics and experimental evolution that occurred at the Station. But its evolutionary motivations were also murky: while the research relied upon the shared evolutionary history of two mammals, the rats here were studied in a situation they would never encounter. It was also based on perceived psychological similarities between rats and humans along with the experimental control available to rat studies. It was *eugenical*, however, and it was important enough to be conducted for six to seven years.<sup>396</sup> (The Station also intended to test temperature and humidity, installing an air-conditioner that failed.<sup>397</sup>) The conclusion of the project was that alcohol did have negative hereditary effects.

Besides the basic tenets of Mendelian inheritance, another certainty that emerged from the Station's researchers and other CIW-funded biologists was the falsehood of neo-Lamarckism, specifically the inheritance of acquired characters. In 1908, C. C. Guthrie published work on ovary transplantation in chickens, claiming to demonstrate an experimental example of the inheritance of an acquired character, namely color. After transplanting ovaries from white chickens to black chickens (and vice versa), Guthrie observed that some chicks showed the influence of the foster mother's color, concluding that the ovary and its eggs were directly affected by their new environment. Upon reading this result, and of similar experiments on rabbits, Davenport and Castle (funded with \$1,000 by CIW) replicated the experiments in chickens, guinea pigs, and frogs, but not the results. Davenport concluded that Guthrie had not actually shown the chicks were from the transplanted ovary; instead, it was possible that the foster mother never "became functional" and the removed ovary had regenerated. Castle and Phillips succeeded in making the transplanted ovary functional, and with their more rigorous genetics work, showed that the offspring of the foster mother instead matched the original owner of the ovary. They emphasized, "*we can detect no modification.*"<sup>398</sup> Castle reported to CIW that

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<sup>395</sup> CIW Yearbook, Vol. 12, 1913, p. 115. Referencing maize is curious given Shull's upending of that commonplace.

<sup>396</sup> CIW Yearbook, Vol. 20, 1921.

<sup>397</sup> CIW Yearbook, Vol. 14, 1915, p. 132.

<sup>398</sup> Guthrie, "Further Results of Transplantation of Ovaries in Chickens," *Journal of Experimental Zoology* 5 (1908): 563–576; Davenport, "The Transplantation of Ovaries in Chickens," *Journal of Morphology* 22 (1911): 111–122; Castle and Phillips, "A Successful Ovarian Transplantation in the Guinea-Pig, and Its Bearing on Problems of Genetics," *Science* 30 (1909): 312–13. They continued the work with CIW funds, confirming their conclusion: Castle and Phillips, "On Germinal Transplantation in Vertebrates," *Carnegie Institution of Washington* 144 (1911); Castle and Phillips, "Further Experiments on Ovarian Transplantation

this work, instead of confirming neo-Lamarckism, “affords the strongest existing experimental evidence in support of Weismann’s postulate” of a separation between germ and soma.<sup>399</sup> While this work has not been discussed by historians, it follows what Peter Bowler has argued generally: the experimental turn in biology brought about Lamarckism’s downfall.<sup>400</sup>

For another line of research investigating use and disuse, Davenport hired Arthur Banta to conduct studies in the Station’s mostly unused “artificial cave.” The purpose was to study “the way in which body pigment is lost, eyes degenerate or disappear, and tactile organs hypertrophy in animals inhabiting caves, abysmal waters, and other dark situations. ... The artificial cave affords conditions approximating those of a natural cavern.” Recapitulating the Station’s initial years, Banta spent considerable time collecting species and working out how to maintain them. In following reports, the sheer number of species under study — mud minnows, crayfish, salamanders, wood-frogs, amphipods, isopods — obscured the conclusions at which Banta arrived. But by 1915, “enough ha[d] been seen” to determine that differences between unpigmented cave forms and pigmented forms were likely genetic, not lost due to “disuse.”<sup>401</sup>

Two resident investigators illustrate the broader notion of experimental evolution conducted by the Station — statistician James Arthur Harris and biochemist Ross Aiken Gortner. Harris, who had arrived at the Station in 1907, carried on the biometrical tradition of Weldon and Pearson as well as their anti-genetic tendencies. Harris’ extensive statistical studies attempted to correlate “selective elimination” and fecundity with botanical traits, including ovule and leaf size and the placement of beans within a pod. Gortner’s research was dedicated to the “great gap” “between the determiners in the germ-cells and the adult characters.” That is, he worked to decipher the links between genotype and phenotype, or in a sense, the biochemical pathways that linked genetics and biometry — the “chemistry of ontogeny.” In Davenport’s view, this was linked to experimental evolution through heredity as “the control or direction of ontogeny.”<sup>402</sup>

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in Guinea Pigs,” *Science* 38 (1913): 783–86.

<sup>399</sup> CIW Yearbook, Vol. 9, 1910, p. 240. See also CIW Yearbook, Vol. 10, 1911, p. 240.

<sup>400</sup> Peter Bowler, *The Eclipse of Darwinism* (Baltimore: Johns Hopkins University Press, 1983), 102.

<sup>401</sup> CIW Yearbook, Vol. 9, 1910, p. 82; Vol. 12, 1913, pp. 111–112; Vol. 14, 1915, p. 145.

<sup>402</sup> CIW Yearbook, Vol. 14, 1915, p. 128. Davenport explained in 1907 that “more and more it becomes clear that problems of inheritance are chemical problems, and that the development of this or that



Harris found statistical correlations between physiological and morphological variations, while Gortner dedicated much of his time to studying the biochemical pathways of pigmentation (the most common trait for Mendelian studies). Thus, both Gortner and Harris fulfilled supplementary roles in the Station, both conducting their own research but frequently collaborating with others.

Shull's return to the Station on a more permanent basis after his work with Burbank lasted only several years, taking a position in Princeton in 1915 and replaced by Albert Blakeslee, the Station's future director. Blakeslee initially focused on mutation induction by chemicals in *mucors* (a genus of fungal mold).<sup>403</sup> Adopting *Datura* (jimsonweed) in the 1920s helped him realize Davenport's goals of mutation induction using the chemical colchicine, discussed extensively by Helen Anne Curry.<sup>404</sup>

World War I pulled away the resident scientists and assistants in 1917-1918 through conscription and applied scientific research. Davenport remained in the U.S., serving on the National Research Council's Anthropology committee, developing selection criteria for naval officers. MacDowell, a Quaker, worked in the Red Cross' reconstruction unit in France. Metz researched malarial mosquitoes for the Public Health Service and Riddle was a captain of the Army's Sanitary Corps. Two others remained in the U.S. because of children (presumably Harris and Banta) and Blakeslee, working under the National Research Council, expanded his "extensive project for perfecting a superior race of prolific [adzuki] beans."<sup>405</sup> Most of the assistants went to war (one of whom died) and were replaced with women (although a number of women already

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characteristic of the adult is to the presence of a specific enzyme in the germ cells. Thus an albino mouse may be derived from a gray mouse, a black mouse, or a chocolate mouse. ... Indeed the fact, that the enzymes of the germ cells and particularly of the egg determine hereditary characters, points the way to the modification of hereditary qualities, and to the production of this or that character at will. Such, at least, is the goal of the investigator." Davenport, "Recent Advances in the Theory of Breeding," *Proceedings of the American Breeders' Association* 3 (1907): 132-135.

<sup>403</sup> CIW Yearbook, Vol. 12, 1913, pp. 104-105.

<sup>404</sup> Helen Anne Curry, *Evolution Made to Order: Plant Breeding and Technological Innovation in Twentieth Century America* (Chicago: University of Chicago Press, 2016). Given Curry's as well as Luis Campos' extensive histories of induced mutation research in the 1920s, I do not discuss them in-depth in this dissertation.

<sup>405</sup> CIW Yearbook, Vol. 17, 1918, pp. 104, 104. Here Blakeslee noted that the work was a "primarily a practical problem with relatively little theoretical interest," but there was research on seed-color, in hopes of finding a correlation to yield, "but also satisfy the market requirements in respect to seed appearance," a cultural criterion. There were also the selective criteria of palatability.

worked there), who mostly maintained stocks.<sup>406</sup> The Station itself supplied mice for laboratory studies. Gregg Mittman has written about biologists' desire and struggle to match physical scientists' considerable contributions to the war effort, and the trajectories of Station scientists reflect that: from the most well-funded biological laboratory in the country, only Blakeslee brought experimental evolution to bear upon it.<sup>407</sup>

By 1920, the Station combined genetics and eugenics to an increasing degree. In 1919, of the thirteen accomplishments Davenport listed, only two or three were explicitly *experimental evolution*; most were eugenics, genetics, and biostatistical. In his 1920 review of the Station's research, Davenport suggested that "the work of the Station for Experimental Evolution and that of the Eugenics Record Office are so akin and so interdependent that they should obviously be united in one department of Genetics." He lamented, "that our highest hopes for the Station have all been realized can not be affirmed." Still, Davenport claimed for the Station "the first discovery the variation of chromosomes associated with, and inducing, a corresponding mutation of a species (the evening primrose)," opening the path for Morgan's lab. Station workers had isolated "types of mutations — ... interchromosomal mutations and intrachromosomal mutations." The Station also confirmed that "evolution has proceeded not primarily by modifications" of somas, but by "changes in the 'germ-plasm,' the chromosomes," sometimes spontaneously, sometimes by induced changes via hybridization or changed conditions.<sup>408</sup>

It is rather apparent that the increasing focus on chromosomes was the hallmark of the Station's research. Davenport wrote,

Mankind is what it is in its physical, mental, and temperamental aspects because of the antecedent changes that occurred in the chromosomes of man's ancestors; and even inside of the "human" group, by changes in genes, numerous inheritable subgroups or "biotypes" have arisen with their physical, mental, and temperamental peculiarities. All these conclusions, which arise naturally and inevitably from experiments and

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<sup>406</sup> CIW Yearbook, Vol. 17, 1918, pp. 103-104.

<sup>407</sup> Gregg Mitman, *The State of Nature: Ecology, Community and American Social Thought, 1900—1950* (Chicago: Chicago University Press, 1992). The Station's contribution to WW1 contrasts with that of WW2 in which under Demerec it led a project on penicillin.

<sup>408</sup> CIW Yearbook, Vol. 18, 1919, p. 123; Vol. 19, 1920, p. 108. CIW had purchased the Eugenics Record Office in 1918. Davenport also suggested the Station should primarily occupy itself with mammals, to study temperament, cancer, color, and fecundity.

observations in which this country has taken a leading part, are bound to revolutionize man's attitude toward himself, toward racial differences, and toward those aberrant individuals who constitute so great a "social problem."<sup>409</sup>

Renaming the Department of Experimental Evolution to the Department of Genetics made sense, given the Station's growing focus on genetics and eugenics.<sup>410</sup> Eugenics was not experimental in the traditional sense, but relied on pedigrees of traits and statistical analyses of "human mate-selection, differential fecundity, and the sex ratio." It was the "genetics of man."<sup>411</sup> Experimentally, Davenport desired to "push the study of inheritance of instincts (in dogs), of tumor-growth (in mice), of sex ratio, of the meaning of sex and sex intergrades, of fecundity, of sterility, of particular traits in animals and plants." In Davenport's view, "the experiments of the department proper with plants and animals are thus supplemented very advantageously" by the pedigrees of human heredity.<sup>412</sup>

From 1909 to 1920, grant funding more than doubled from \$29,000 to \$78,343.27 and capital funding more than tripled from \$46,005.86 to \$161,199.99.<sup>413</sup> Following the end of the war, money at CIW became quite tight from their contributions to governmental research, forcing Woodward to request Davenport reduce the Station's expenses by more than a tenth. Davenport's projected expenses for 1920 dedicated \$58,280 to salaries distributed among 34 employees. In addition to Davenport (\$7,200) and six investigators (between \$3,000 and \$3,720 each), there were: a research associate for Metz, superintendent, carpenter, mechanic, stenographer, engineer, "greenhouse man" and greenhouse laborer, nine assistants to the investigators (six of whom were women) three computers (all women), a poultryman, farmer, laborer, an artist, and summer assistants (unknown number).<sup>414</sup> This was substantial growth from the less than dozen

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<sup>409</sup> CIW Yearbook, Vol. 19, 1920, pp. 107-108.

<sup>410</sup> Davenport's initial proposal included a section of *Drosophila* Investigations, supervised by Morgan, who was already receiving \$3,600 per year from CIW, as well as one for biometry. Davenport to Woodward (1919/3/3) and (1919/5/7), APS Davenport, Box 105, "Woodward, R. S. 1919 Folder 2, March - June."

<sup>411</sup> Davenport to Woodward (1919/2/10), APS Davenport, Box 105, "Woodward, R. S. 1919 Folder 1, January - February." I say "in the traditional sense," because it can be argued that eugenical laws and practices were interventions on the genetics of the population — an "experiment on a gigantic scale."

<sup>412</sup> CIW Yearbook, Vol. 19, 1920, p. 109; Vol. 11, 1912, p. 19.

<sup>413</sup> In 2017 dollars, \$2,908,522.29. ERO funding in 1920 totaled \$218,491.90; in 2017 dollars, \$2,652,917.73. Total of SEE + ERO in 1920 in 2017 dollars was \$5,561,440.02.

<sup>414</sup> Woodward to Davenport (1919/10/9), APS Davenport, "Woodward, R. S. 1919 Folder 5, October – November"; Davenport to Metz (1919/12/31), "Woodward, R. S. 1919 Folder 6, December"; "Estimated Expenses for 1920," APS Davenport, "Woodward, R. S. 1919 Folder 6, December."

employees at its founding and showed CIW's commitment to the science.

Throughout the 1920s under Davenport's leadership, the now Department of Genetics continued its focus on chromosomes, mutations, and eugenics with other projects including the genetics of leukemia and how to control sex ratios and sex determination. Under Blakeslee and then Milislav Demerec in the late 1930s onward, eugenics dropped out and the Cold Spring Harbor Laboratory became a center of *Drosophila*, maize, phage, and microbial genetics, hiring and hosting biologists such as Barbara McClintock, Dobzhansky, Delbruck and Luria, among many others.

### Conclusion

In its first fifteen years, the Station had partially fulfilled Davenport's vision of a New Atlantis. It had certainly received the financial support and built the infrastructure that biologists had argued were necessary for a program in experimental evolution. The Carnegie Institute of Washington's interest in the control of evolution meant pouring enormous sums into experimental biology and creating a network of scientists dependent on its resources. Like Woods Hole, it had also become a center for students to train and for scientists to conduct summer projects. Davenport succeeded in creating his vision, at least socially.

Scientifically, the Station's work appears quite messy, reflective of the state of the evolutionary sciences at the time. Davenport's application materials alone demonstrate the plethora of vying theories and mechanisms in the early twentieth century. While the following two chapters also demonstrate that natural selection was far from ignored and biologist's understanding of its dynamics developed immensely, it is interesting how small a role it played in the work of the Station proper aside from Shull. This is especially odd given selection's prominent role in breeding, and indeed, Davenport's increasingly rare non-eugenics scientific work – sheep breeding (mentioned above) – did involve the Mendelian theory of selection. Perhaps he thought CIW grantee William Castle (and the debate) sufficiently covered the topic. This is further supported by the Station hiring Castle's student E. C. MacDowell, who carried out selection experiments on *Drosophila*

(that contradicted Castle, discussed in Chapter 5).<sup>415</sup> The “eclipse of Darwinism” meant there was initially no reigning paradigm to center the work; instead, what guided the Station’s diverse research was an ideology of experimentation and the potential for future control of the evolutionary process. The result was the elimination of some theories and mechanisms as contenders that did not survive experimental treatment, particularly neo-Lamarckism, and an emphasis on the more (potentially) manipulable elements of variation and heredity, namely the chromosomes.

In 1916, Davenport wrote about “the form of evolutionary theory that modern genetical research seems to favor.”<sup>416</sup> In addition to paleontological and embryological results, as well as analogies to radioactive decay, Davenport pointed to the results of “experimental breeding.”<sup>417</sup>

The core result was the “primacy of internal factors.” Read back into the nautical metaphor that appeared in his application materials, Davenport argued that the Station had demonstrated that evolution was more like a steamship, acting independently of the environment, rather than a canal boat. Experimental evolution had elucidated four principles: (1) variations among related organisms are parallel, such as the genetics of coat color in rabbits and guinea pigs or mutations in species of *Drosophila*; (2) mutations were not multifarious, but limited, as shown by Harris’ examination of variation in over a million bean seedlings; (3) most mutations are losses; and (4) “many mutations begin small and can be rapidly evolved into highly developed characters,” a phenomenon discussed extensively in the next chapter through William Castle’s polydactylous guinea pigs.<sup>418</sup> If evolution proceeded primarily through internal factors, Davenport explained that adaptation was not so much created or “brought about,” but occurred through the “absence of non-adaptiveness,” a de Vriesian position based also on Darwin’s position

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<sup>415</sup> MacDowell spent 38 years at the Station, retiring in 1952. After *Drosophila*, he took up the effects of alcohol in mice through the 1920s, and due to a serendipitous development in his cultures, dedicated the rest of his career to understanding the genetics of leukemia. CIW Year Book XYZ

<sup>416</sup> Charles Davenport, “The Form of Evolutionary Theory That Modern Genetical Research Seems to Favor,” *The American Naturalist* 50, no. 596 (1916): 449–65.

<sup>417</sup> Luis Campos has highlighted the context in which the analogy to radioactive decay was made. Luis Campos, *Radium and the Secret of Life* (Chicago: University of Chicago Press, 2015), 116–17.

<sup>418</sup> For this fourth principle, Davenport cited four lines of evidence, two of which were from experiments conducted at the Station by Davenport and Frank Lutz, another by Castle partially funded by the CIW, and the fourth by de Vries. Regarding the third principle, specifically, Davenport alluded to the theory of William Bateson’s. Note also that Davenport subscribed to the presence and absence theory of genetics.

that variation did not respond to specific conditions. The role of natural selection, then, depended largely upon the degree to which the soma reflected the germ, the index between phenotype and genotype.

The “form” of the evolutionary theory Davenport thought conformed to the evidence best was then a combination of genetic reductionism and orthogenesis. Whatever differences existed among geneticists, he wrote, “upon one point all geneticists are ... agreed — that we must interpret all of our results in terms of our genes alone.” (Note Davenport’s easy extension from genetics to eugenics.) The orthogenetic aspect was two-fold:

A theory of evolution that assumes internal changes chiefly independent of external conditions, i.e., spontaneously arising, and which proceeds chiefly by a splitting up of and loss of genes from a primitively complex molecular condition of the germ plasm seems best to meet the present state of our knowledge.<sup>419</sup>

Because mutations remained spontaneous, and selection was dependent upon their occurrence *and* their clear expression in the soma, experimental evolution was at somewhat of an impasse, a notion expressed by several experimentalists in the following chapters. Davenport wrote, the resulting theory “renders less hopeful (but not hopeless) the prospect of being able to control completely by experimental methods evolutionary change.” He remained open to the possibility that the “germ plasm is not beyond the reach of modifying agents,” and suggested the continuation of experiments along those lines.

While I have not discussed eugenics, and Davenport did not tie this theory explicitly to eugenics, it does seem to fit the general ideas of eugenics from the time. Genetic reductionism eliminated the importance of environmental effects and variation, critical to justifying eugenical laws in capitalist society. The notion that evolution proceeded through loss also pointed to the need to restrict who was permitted to contribute to the following generation. For Davenport, “loss” did not necessarily entail degeneration, although that was one direction it could take.<sup>420</sup>

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<sup>419</sup> Davenport, 1916, p. 463. This view seems reminiscent of Bateson’s theory of evolution by decay.

<sup>420</sup> After all he had to explain the diversity and complexity of life and all of its specializations, which he did by pointing to the possibility that “the loss is not merely of a whole gene, but of some part of it; a fractionation, as it were, by which the gene becomes altered or split up into two or more.”

As much as the results of the Station's work, in Davenport's view, appeared to not have produced the active control of evolution, to argue that it was a failure would be to succumb to the belief that positive results are all that matter. The other side of "the primacy of internal factors" was the elimination of external-based theories of evolution, namely, neo-Lamarckism.

This restrictive view of evolution was not present at the Station's founding — instead, the resident scientists considered a plethora of evolutionary theories. A focus on early twentieth-century experimental evolution shows that a reading of this period as the "eclipse of Darwinism" undersells and in fact misunderstands the period. One major consequence of focusing on experimentation is that debates within evolution appear far less partisan and the experimental biologists advocate multi-causal, not monocausal, accounts. That is, the Station engaged with several mechanisms and theories in a fair way: whereas Weismann, who in a polemical experiment sliced off rats' tails to disprove a neo-Lamarckian strawman, Davenport and Castle replicated the experimental procedures of a neo-Lamarckian. Davenport, Tower, Johnson, Frank Lutz, and others considered seriously and experimented with natural and artificial selection, orthogenesis, neo-Lamarckism, direct effects, organic selection, mutationism, and Mendelism. Of what entered the Station in 1904, though, only mutationism and Mendelism exited, combined with a unique take on orthogenesis. This to some degree matched the results of the debates over selection and mutation about pure line theory, which Davenport referenced directly in 1916. I focus on this debate for the last two chapters of the dissertation

CIW and Davenport built the Station for Experimental Evolution to test theories through practice. Many scientists had argued that evolutionary science's theoretical morass could be solved only through experimentation on a large scale. It needed significant capital investment to afford the physical infrastructure, the laboratory and agricultural populations of animals and plants, and the resident scientific and caretaking personnel to carry out the long-term experimentation. Thus in this case private capital was necessary for the work to even take place, especially before the explosion of public funding that began during World War 2. The Station itself occupied a mediating space between science and (agricultural, later eugenic) society, searching for and testing laws that governed evolution's control. The theories the Station tested were an eclectic mixture

of ideas produced by scientists, breeders, and farmers to explain the changing material they witnessed and even controlled – but only to some extent. The result was the elimination of most theories that emphasized the environment and the promulgation of theories that emphasized internal factors such as genes and chromosomes. As the next chapters discuss, selection, itself a mediation between the external environment and the internal organism, was in turn reshaped to be the mechanical operation of the environment, rather than creative, choosing between differences independently thrown up by the genetic material (rather than creating the differences itself). Therefore, in the view of an important segment of American geneticists and experimental evolutionists, the Station had helped take theories accumulated by practice, and through the particular practices of experimental evolution, condensed a new theory and threw out the rest.



## Chapter 4: Controlling Evolution?: Mutationism, Pure Line Work, and Genetic Selectionism

### Introduction

Although the development of experimental evolution in the early twentieth century was rather messy, exemplified by Davenport's Station for Experimental Evolution, there also emerged a coherent and intense debate on the interactions and relative creative powers among heredity, variation, and selection. The debate centered upon theories rooted in experimentation, such as pure line theory and gametic contamination, each competitor having major implications for how to control evolution and especially *the degree* to which it could be controlled, if at all.

This chapter introduces a few of the scientists involved: Harvard geneticist William Castle, an early adoptee of Mendelism whose experimental evolution led him to formulate the theory of gametic contamination, elevating the power of selection over mutation; botanists George Shull (Station for Experimental Evolution) and Edward Murray East (Connecticut Agricultural Experimental Station, then Harvard), whose breeding experiments eventually helped produce hybrid maize, based on the mutationist and pure line theories of Hugo de Vries and Wilhelm Johannsen; and Johns Hopkins protozoologist Herbert Spencer Jennings, who independently formulated a pure line theory that limited the power of selection. The next chapter follows these scientists, experiments, and theories as they clashed and as other scientists, such as Morgan's laboratory, entered the fray.<sup>421</sup>

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<sup>421</sup> Raymond Pearl would have fit perfectly as one of the main actors in Chapters 4, but I concluded that his work offered little narrative contrast with what I had already included. He does feature prominently as a debate participant in Chapter 5, however. For his work, see "Inheritance of Fecundity in the Domestic Fowl," *American Naturalist* 45, no. 534 (1911): 321–45; "The Mendelian Inheritance of Fecundity in the Domestic Fowl," *American Naturalist* 46, no. 552 (1912): 697–711; "Seventeen Years Selection of a Character Showing Sex-Linked Mendelian Inheritance," *American Naturalist* 49, no. 586 (1915): 595–608; "Fecundity in the Domestic Fowl and the Selection Problem," *American Naturalist* 50, no. 590 (1916): 89–105. Kathy J. Cooke has examined Pearl's relationship to agriculture and practice; see "From Science to Practice, or Practice to Science? Chickens and Eggs in Raymond Pearl's Agricultural Breeding Research, 1907-1916," *Isis* 88, no. 1 (1997): 62-86. Kyung-Man Kim interestingly suggests that Pearl's work had established the necessary terms for the breeder's equation, although Pearl never put them together in that way (e.g., heritability, response to selection, and selection differential); see *Explaining Scientific Consensus* (New York: The Guilford Press, 1994), 136-138.

In this chapter, I argue that the period from about 1900 to 1920 is best understood not only as the formative era of genetics, but also as the era of experimental evolution. In the previous chapter, I showed that Charles Davenport had envisioned experimental evolution broadly, which included Mendelism, pure line theory, mutationism, natural and artificial selection, and hybridization. In some ways, experimental evolution and genetics became fused by 1920, but I argue that the framing of “experimental evolution” is more explanatory of this preceding period. Much of what follows precedes the paradigm-setting chromosome research of the Morgan laboratory, for example. Rather, the “geneticist” figures examined in this chapter — Castle, East, and Shull — were primarily concerned with how the experimental sciences of heredity and variation interacted with evolution, and *especially selection*, both natural and artificial. This can be explained largely due to their second (but not *secondary*) focus: systematic breeding, the control of the evolution of crops and livestock. Instead of treating genetics as a static science, such as confirming Mendelian ratios or mapping chromosomes, these scientists endeavored to witness and control evolution within the experimental laboratory or agricultural field. This is also shown by the Morgan laboratory’s underappreciated preoccupation with evolution. Thus, genetic science has a subservient role to evolutionary science.

Their experimental work had profound impacts on the history of evolutionary theory. As I have explained, Arlin Stoltzfus and I have argued that the mainstream history of biology has underplayed the influence of the early twentieth-century Mendelians and mutationists, painting them as having concocted absurd theories of species-creating mutations that negated the role of natural selection. These chapters build on the “forgotten synthesis” thesis by investigating how another set of biologists engaged with these same critiques of Darwinian theory (through Darwinian method!) and Mendelian-mutationist notions of mutation and selection.<sup>422</sup> The biologists discussed in the paper by Stoltzfus and myself — Bateson, Morgan, de Vries, and Johannsen — were perceived as advocating hardline and totalizing positions. Castle, East, Shull, Jennings, as well as Raymond Pearl and Morgan’s students, in contrast, developed and changed their views in response to experimental results. (This was also characteristic of Charles Davenport.)

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<sup>422</sup> Arlin Stoltzfus and Kele Cable, “Mendelian-Mutationism: The Forgotten Evolutionary Synthesis,” *Journal of the History of Biology* 47, no. 4 (November 2014): 501–46.

This chapter thus shows how the experimentalists' theories developed out of practice; for a majority, their theoretical positions at the end of this period, as they concluded long-term experimental work, contradicted their position at its beginning.<sup>423</sup> Specifically, Castle and Jennings moved from Mendelian-mutationism and pure line theory to a genetic Darwinism, whereas East and Shull moved from a lukewarm Darwinism to Mendelian-mutationism.<sup>424</sup> Keeping in mind that the theories these biologist took recourse to also had their own practice-driven history. Thus, a history of experimental evolution reveals a dichotomy between hardline theory-makers and open-minded experimentalists – a focus on the former, through a history of ideas, distorts the field's broader history.

These chapters also build on the dissertation's goal of establishing the central concern among biologists of taking control of evolution. All agreed that experiment, theory, and application were deeply intertwined. They adopted the Darwinian and Mendelian tradition that artificial experimental work in the guise of breeding provided knowledge on how evolution operated both under human practice and in nature (although this latter concern received less emphasis, which I discuss throughout). As in Davenport's history of experimental evolution, they also worked in the tradition of breeders, particularly Louis de Vilmorin, Nils Heribert-Nilsson, Willet Hays, as well as their experimentalist interpreters Hugo de Vries and Wilhelm Johannsen. Particularly striking is how experimental work produced theories, selectionism versus mutationism (broadly), that conflicted on how evolution worked and how evolution could best be controlled. I show specifically that most of them were worried about the implications of mutationism in *limiting* human control. The point being that the desire to control evolution was not at all new, but with the biologists in these two chapters, *how best to control evolution became a point of dispute*. To be specific, their concern hinged on whether mutation or selection were the creative factors of evolution.

I will briefly note that while this concern has faded with time, the notion of

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<sup>423</sup> In parallel, Kim (1994) shows how most relevant biologists switched from Pearsonian biometry to Mendelism, and rarely the other direction.

<sup>424</sup> Although Castle at the very end of this period, in 1919, conceded that his experiments did not demonstrate his theory of genetic Darwinism, which is where the body of my dissertation comes to an end in Chapter 4/5.

“creativity” was important to many evolutionary scientists in this period. Darwin had compared natural selection to an architect building with formless matter, an evocative description of his view of evolution. Mutationists instead compared selection to a censor or a sieve, reflecting their view that selection eliminated variation, but did not create that variation. Whichever process in evolution held the creative agency was then its dominant factor, but that did not necessarily mean it could be controlled.<sup>425</sup>

That they had practical concerns is not so surprising when considering the institutional context. Castle was funded by the Carnegie Institution of Washington and worked at Harvard University’s Bussey Institution. East began his career at the Illinois and Connecticut Agricultural Experiment Stations and later joined Castle at Harvard and Bussey. Shull was a resident scientist at the Station for Experimental Evolution directed by Charles Davenport. Jennings worked at a variety of colleges and universities throughout his early career, and even served briefly as acting director of the U.S. Fish Commission at the Great Lakes Biological Survey, but for the duration of these chapters, he was Professor of Experimental Zoology at Johns Hopkins University, thus the most purely academic of this set.<sup>426</sup> (This is consistent with Barbara Kimmelman’s study of early genetics arising primarily at land-grant agricultural colleges.<sup>427</sup>) CIW and Charles Davenport’s Station thus loom large as a proxy organizers of this debate, and even partially funded both sides of the debate: Davenport mentored Castle and Jennings; Davenport employed Shull; and CIW provided grants to Castle and later the Morgan laboratory. Most of this work did not occur at the Station for Experimental Evolution,

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<sup>425</sup> Stoltzfus and Cable, “Mendelian-Mutationism: The Forgotten Evolutionary Synthesis” (2014) and John Beatty, “The Creativity of Natural Selection? Part I: Darwin, Darwinism, and the Mutationists,” *Journal of the History of Biology* 49 (2016): 659–684. My undergraduate senior thesis was also on the historical perceptions of creativity in evolution.

<sup>426</sup> Jennings was the successor to W. K. Brooks as Director of the Zoological Laboratory. Before taking this position, he was being courted by the Rockefeller Institute, but not to do experimental evolution, but studies of cell growth and division. He ultimately lost this opportunity to his rival Jacques Loeb. The President of CIW’s Executive Committee had steered him towards CIW, but this too failed. He nearly lost the directorship to Morgan as well. See Sharon Kingsland, “A Man Out of Place: Herbert Spencer Jennings at Johns Hopkins, 1906-1938,” *American Zoology* 27: 807-817 (1987). Raymond Pearl, a former student of Jennings, worked for the Maine Agricultural Experiment Station and later joined Jennings at Johns Hopkins where he took up public health and biostatistics.

<sup>427</sup> Barbara Kimmelman, “A Progressive Era Discipline: Genetics at American Agricultural Colleges and Experiment Stations, 1900-1920,” PhD diss., (University of Pennsylvania, 1987). The Morgan laboratory plays an important role in the following chapter as Sturtevant, Bridges, and Muller become involved in the debate with Castle.

showing the importance of CIW's funding network established by Davenport.

This area of experimental evolution linked the immediately practical work of agricultural experiment stations with the academic biology more interested in the workings of nature. East, Shull, and Pearl worked on maize, potatoes, and poultry, contributing to Johannsen's pure line theory that had its own origins in practical concerns. Castle's choice of small mammals, especially color, may have had useful applications in breeding, but this was not emphasized. Jennings at Johns Hopkins was able to conduct long-term experimentation on non-medical microorganisms. Through their combination of research through collaboration, corroboration, and dispute, this area of experimental evolution was able to continue the Darwinian and Mendelian methodological traditions of examining both artificial and natural evolution.

There were important theoretical developments, again linked to practical work. Experimental evolution required the use of populations, whether a field of maize or *Paramecia* in petri dishes, and this necessity encouraged a transition from "typological thinking" to "population thinking." A dichotomy proposed by Ernst Mayr, early geneticists are usually lumped together as "typological thinkers" who missed, or rejected, a key component of Darwinism (as interpreted by the architects of the Modern Synthesis). The population thinking that emerged from these scientists is not identical with that of Fisher, Mayr, or Dobzhansky in that they saw selection as deciding between types within a population. But Mayr's static dichotomy misses that East, Shull, Castle, Jennings, and others investigated the dynamics of selection within populations. As Stoltzfus and I argued respecting natural selection, the interrogation of genetic and evolutionary mechanics required a new understanding of populations and points to the critical theoretical developments that emerged from experimental evolution.

I argue, therefore, that the history of evolutionary science was shaped by institutional and scientific interests and desires in controlling it. The impact was profound enough, that, to put it strongly, evolutionary science "reset."<sup>428</sup> Instead of merely elaborating upon Darwin's ideas, what emerged from this period were *new* theories of

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<sup>428</sup> A better phrase would be the Hegelian term "sublation" (*Aufhebung*) in which a critique of the old brings forth the new, but not with an absolute demarcation, but by also preserving it (e.g., Newton and Einstein).

variation, *new* theories of heredity, a *new* conception of natural selection, along with subsidiary theories of mutation, sex, and inbreeding (and, in addition, chromosomal mechanics). Where they were potentially weakest — adaptation and speciation — is also then not surprising: for the former, adaptation consisted of (socially-shaped) breeder desires and was therefore built into the experiment.<sup>429</sup> The traditional view of their disregard for these problems is not entirely incorrect, but that they rejected selection as an important factor in evolution is decidedly incorrect.

This chapter begins with the work of William Ernest Castle (1867-1962) as his experimental evolutionary research on small mammals initially confirmed the importance of mutations, but gave way to a genetic Darwinism, opposed to most of his colleagues. Known for mentoring Sewall Wright and for his dispute with pure line theory, this chapter highlights his early experimental evolution work prior to the hooded rats and their roles in convincing him of that the genetic factors could themselves be changed by natural selection through a process he called “gametic contamination.” Working at Harvard University’s Bussey Institution, Castle’s work was funded by the Carnegie Institution of Washington (CIW) for four decades (1904-1943).<sup>430</sup> Although Castle himself rejected Mendelian-mutationism, his vehement opposition to the theory drove this section of experimental evolution forward until he conceded in 1919 that genes were immune to selection.

The work of botanists Edward Murray East (1879-1938) and George Harrison Shull (1857-1954) provides the contrast to Castle, as they began their experimental evolution work loosely attached to Darwinism and selectionism but abandoned it as they took up the theories of de Vries and Johannsen. Their primary focus — crop breeding, especially of maize — motivated their interest in these theories, theories borne from experimentation and conceptualization of breeding practices. Both are known for their contributions to hybrid corn, which they conducted in the spirit of experimental evolution.

The chapter concludes with the work of Herbert Spencer Jennings, the odd duck

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<sup>429</sup> Questions of adaptation were a focus of experimental evolutionists who worked in the field, but as Kohler emphasizes, this sort of hybrid work proved to be difficult to conduct.

<sup>430</sup> L. C. Dunn, “Castle, William Ernest,” *Biographical Memoirs of the National Academy of Sciences*, 1965, 40.

of this cohort. His entire career was primarily dedicated to microorganisms, initially their behavior and then how they illustrated evolution at work. Given the state of microbiological research outside of medicine, his work had the least obvious applications, yet his colleagues treated it as theoretically valuable in their practice-oriented debate. His work thus serves as a contrast to the desire to control, showing possibly that experimental evolution need *not* be tied so explicitly to material and economic interests, although I show that it clearly was historically. He did share rather parallel worries to Castle, East, and Shull, in that his experimental results in support of pure line theory left him puzzled as to how evolution in nature could even work, which I call “Jennings’ Problem.”

Experimental evolution was the intersection of theory and practice, natural science and breeding, and control. While much has been made of the disputes among evolutionists regarding the relative roles of mutation and natural selection in the early twentieth century, rather less attention has been paid to how these scientists viewed these debates through the prism of application. For them, there was little to no distinction, just as Darwin argued domesticated species were essential to understanding the action of selection as well as the rules of heredity and variation. Thus, this chapter and the following show that 1900-1920 was the era of experimentalism in the evolutionary sciences and critically shaped its future.

### **Castle: From Mendel to Darwin**

Upon reading William Bateson’s defense of Mendel, William Castle adopted the genetics of small mammals as his lifelong field of study with experimental evolution being his focus through 1920.<sup>431</sup> He was among the first American biologists to fully accept Mendelism, publishing seven papers on the subject in 1903. Castle had worked as an assistant for Davenport at Harvard in the 1890s (where Herbert Spencer Jennings was a fellow student), both sharing an early interest in heredity and evolution. His early summaries of Mendelism emphasized its core tenets but identified a number of exceptions, including distinct and stable hybrid classes, mosaic inheritance, and the

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<sup>431</sup> William Provine, *Sewall Wright and Evolutionary Biology* (Chicago: The University of Chicago Press, 1986), 36.

coupling or separation (“disintegration”) of two different characters — what he called “suspensions” of the laws of dominance and recessiveness.<sup>432</sup> His attention to exceptions would lead him to reject Mendelian-mutationism in favor of Darwinism, which put him in a productive conflict with Morgan, among others, although he continued to accept, teach, and publish on the basic Mendelian framework.

In his first years as a Mendelian, Castle adopted a Batesonian view of variation and selection. He agreed with Bateson that “discontinuous (or sport) variation [w]as of the highest importance in bringing about polymorphism” and speciation.<sup>433</sup> Articulating an early version of the “lucky mutant” scenario, Castle suggested that sports may be common enough that “even if a particular combination of characters is uniformly eliminated by natural selection under one set of conditions, it may reappear again and again, and finally meet with conditions which insure its success.” He even acknowledged, following Bateson, that Mendelism could account for continuous variation: because a cross between tall and short pea plants produces offspring of intermediate height, the original tall and short characters could potentially “disintegrate” into a “dozen classes,” “resulting in a practically continuous frequency-of-error curve.”<sup>434</sup> Castle was well on his way to becoming one of the chief proponents of Mendelian-mutationism.

Castle also followed Darwin and Bateson in believing that scientific theory and breeding practices informed each other. Indeed, Castle argued that “the biologist must himself turn breeder.” Because “the variations of domesticated animals [threw] light on the origin of species,” “the successful practical breeder, the man who originates breeds,” is himself an agent of evolutionary change. In fact, he argued, “there is no essential difference between breeds and species.” This held methodological importance because breeds “are forming under our very eyes all the time and that this has been going on since the early historic times..., yet the method eludes us.” However, breeders usually could not articulate their methods, keeping them private or because they did not know the “real nature of the material used and the processes involved.” Thus, Castle echoed

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<sup>432</sup> W. E. Castle, “Mendel’s Law of Heredity,” *Science* 18, no. 456 (1903): 396–406; W. E. Castle and Glover M. Allen, “The Heredity of Albinism,” *PNAS* 38, no. 21 (1903): 608–9.

<sup>433</sup> Castle, “Mendel’s Law of Heredity,” 404.

<sup>434</sup> Castle, “Mendel’s Law of Heredity,” 405. One of the mysteries of early Mendelism is how frequently this hypothesis was asserted but continually failed to be adopted, including by Castle himself. Later in this chapter I discuss how East claimed to experimentally demonstrate the case; Castle rejected it.



Mendel's own interest in artificial transformation, asserting that Mendelism would transform breeding from an "art" that "consisted largely of groping for treasure in the dark" to a rational and predictable science.<sup>435</sup> Even his verbal articulation of what would become Hardy-Weinberg he called the "law governing race improvement in cases of alternative inheritance."<sup>436</sup> Thus for Castle, the experimentalization of evolution entailed the control of evolution, and vice versa, and would transform the practical knowledge and application of evolution, breeding, from being impressionistic to scientific. To do so, Castle (perhaps unconsciously) adopted the quasi-breeding method of conducting routine work, in this case genetic analysis of guinea pigs, rabbits, rats, and mice, and taking advantage of mutations that arose by chance, and then investigating how selection and the mutation interacted. While Castle began this work as a Mendelian-mutationist, his practical engagement with these mutation-selection experiments converted him to a hardened genetic Darwinism, which the rest of this section will illuminate.

As Castle worked out classical Mendelian inheritance in small mammals, he encountered two mutations or sports that he thought supported a Mendelian-mutationist theory of evolution. The first was a long-haired ("Angora") guinea pig that appeared after inbreeding a "supposedly pure" short-haired stock, shown to be a recessive Mendelian trait.<sup>437</sup> The second sport (mutation) was a polydactylous guinea pig, an apparently novel character. In the following years, Castle developed and fixed these traits in stocks, from which he articulated a synthetic account of evolution, presented to the American Society of Naturalists in 1904.<sup>438</sup>

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<sup>435</sup> Castle, 401. For an example of Mendelism as a rational breeding technique, he suggested that "the task of the practical breeder who seeks to 'establish' or 'fix' a new variety, produced by cross-breeding, in a case involving two variable characters, is simply the isolation and propagation" of the double homozygous recessive, present as one-sixteenth of the second generation.

<sup>436</sup> Castle also engaged in some modeling, showing how selection — here, the complete elimination of homozygotic recessives within a population — had varied results, depending on how long it was practiced. W. E. Castle, "The Laws of Heredity of Galton and Mendel, and Some Laws Governing Race Improvement by Selection," *PNAS* 39, no. 8 (November 1903): 237. Ernst Mayr noted Castle's work but failed to point out Bateson's and Saunders' initial contributions. Ernst Mayr, *The Growth of Biological Thought: Diversity, Evolution, and Inheritance* (Cambridge, Mass: Belknap Press, 1982), 838.

<sup>437</sup> W. E. Castle, "The Heredity of 'Angora' Coat in Mammals," *Science* 18, no. 467 (1903): 760–61. Castle, finding a parallel case in rabbits, generalized that long hair behaves as a recessive trait in mammals, and corrected Darwin's speculation that long hair arose via the direct influence of climate.

<sup>438</sup> Published in April 1905. W. E. Castle, "The Mutation Theory of Organic Evolution, from the Standpoint of Animal Breeding," *Science* 21, no. 536 (1905): 521–25. Castle's fusion of Mendelism, mutationism, and selection — despite his soon disavowal of such views in 1906 — is reminiscent of the historical theory that Arlin Stolfus and I present in our paper, in contradiction to the mythical "mutation theory" that some

At this point, Castle rejected the belief that selectionism and mutationism were mutually exclusive. After all, Darwin had accepted “single variations” and mutationists accepted a role for natural selection. His own experimental breeding demonstrated the case: first, the sudden appearances of a polydactylous guinea pig and a long-haired guinea pig showed the importance of mutations within individuals; second, by breeding and selecting progeny with the “best” extra digits, he established a race “not *created* by selection, though it was *improved* by that means. ... Any amount of selection practised on other families of my guinea-pigs would probably never produce a four-toed race,” and had not yet happened in seven generations.<sup>439</sup> Therefore, mutations furnished the variation for selection to work upon.

From the case of recessive long-haired guinea pigs, Castle theorized the fate of mutations in a state of nature under the evolutionary dynamics of mutation and selection. He suggested a mutation would produce an interbreeding but non-blending “dimorphic species” that would be subject to selection, eliminating the non-advantageous of the two (although it could possibly survive in another area, as in allopatric speciation).<sup>440</sup> Castle contradicted Darwin’s theories of speciation and breeding, arguing that breeders usually “discovered” new breeds or created new breeds via crossing — “both cases ... mutations, *i.e.*, ... characters *unconnected* by a series of transition stages with the normal form.”<sup>441</sup> Creating a new trait within a breed solely by selection “is an exceedingly difficult and slow process.” Instead, following the mutation’s appearance, selection and crossbreeding “free[d] the stock from undesirable alternative characters” but did not “modify the characters retained.”<sup>442</sup> Castle pointed out, these two traits — extra digits and long hair and their absence — could be combined in four ways, and the “breeder” or “nature” “may

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historians continue to present. That is, Castle did not adopt the cartoon version of de Vriesian mutationism, but instead presented the theory as synthesized by Bateson, Morgan, and Johannsen. Arlin Stoltzfus and Kele Cable, “Mendelian-Mutationism.”

<sup>439</sup> Castle, “The Mutation Theory of Organic Evolution, from the Standpoint of Animal Breeding,” 523. Emphasis original.

<sup>440</sup> Ibid. Note that Castle does not say that the mutation itself creates a species, but instead a dimorphic species; speciation results from the elimination of or separation from one of the morphs. What makes this differ from Darwinism is that the mutation immediately produced two competing varieties; they were not created by selection. The last sentence reflects “segregation to the fittest environment.”

<sup>441</sup> As far as I can tell, Castle is unique here in considering a hybrid to be a mutation. However, it points to the notion that mutations were not characterized by size, but by their non-transitional “unconnected” nature.

<sup>442</sup> Castle, “The Mutation Theory of Organic Evolution, from the Standpoint of Animal Breeding,” 522–24.

now select the particular combination of characters” that best suited the agent’s purpose.<sup>443</sup> The evolutionary theory that resulted was closer to de Vries than to Darwin in which mutations were the basis of variation upon which selection could build or eliminate. This limited both breeders and natural selection to what mutations offered to them.

But as Castle and his students continued to develop these experimental systems — polydactylous and long-haired guinea pigs — in addition to hooded rats and lop-eared rabbits, his interpretations swung the other way, emphasizing selectionism while diminishing Mendelism-mutationism.<sup>444</sup> Specifically, Castle rejected “gametic purity,” in which the hereditary material of both parents remained unaffected by the other. Although he had declared gametic purity “fully substantiated” in 1903, he now announced that it “does not exist.” Instead, he was “certain that the units [of heredity] are capable of modification” through gametic *contamination*.<sup>445</sup> Through gametes’ mutual effect upon each other, selection became the agent of creative change, rather than solely mutation. The switch was apparently stark enough that Castle never once cited his 1904 address (and it does not appear in his collected bibliography by L. C. Dunn).<sup>446</sup>

As Castle abandoned this synthetic approach to evolutionary theory, he also ceased speculating as to how selection worked in nature, instead focusing solely upon artificial selection within the laboratory environment. The irony is that naturalists, not totally incorrectly, accused laboratory geneticists of dismissing the power and ubiquity of natural selection because of their lack of experience in the field. But soon the chief selectionist geneticist, Castle, arguably created the largest divide between nature and the laboratory through his use of intensive inbreeding.

Two of the three results that challenged gametic purity emerged from routine work on Mendelian inheritance: ear length in rabbits and additional results from Angora guinea pigs. When Castle crossed short- and lop-eared rabbits, the following generation (F<sub>2</sub>) did not break apart the characters according to the 3:1 ratio, but were instead

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<sup>443</sup> Castle, 524. Even accounting for his budding skepticism of gametic purity, Castle believed a modified trait could “facilitate the creation of desirable breeds, for it serves to induce new mutation.”

<sup>444</sup> Castle, “The Mutation Theory of Organic Evolution, from the Standpoint of Animal Breeding,” 525.

<sup>445</sup> Castle and Allen, “The Heredity of Albinism,” 620; W. E. Castle, “Yellow Mice and Gametic Purity,” *Science* 24, no. 609 (1906): 280.

<sup>446</sup> [Cite Provine]

homogeneously intermediate, showing no sign of dominance or segregation. He concluded that ear size was a “non-Mendelian character.”<sup>447</sup> Castle also tentatively retracted his claim (upon which the synthetic account of evolution was partially based) that short and Angora hair were Mendelian alternatives in guinea pigs. Although the characters were discontinuous and followed the rules of dominance, expected Mendelian ratios did not appear, leading him to wonder if segregation was incomplete or if the trait was latent.<sup>448</sup> Castle and his student, Alexander Forbes, crossed short- and long-haired stocks, producing only short-haired offspring (as expected in a simple case of dominance), but, in the second generation, individuals had hair lengths that fell between the two categories in a continuous gradation.<sup>449</sup> Although Castle had articulated a possible solution in 1903 — these were the result of multiple factors —, he now concluded there was no Mendelian explanation for the character distributions.

Specifically, Castle interpreted these two results in rabbits and guinea pigs as contrary to the doctrine of gametic purity; in its place Castle substituted *gametic contamination*.<sup>450</sup> It appeared that the two alternative characters, when crossed, somehow affected each other. Intermediate hair length in guinea pigs was transmitted as a “new *creation* due to a partial and permanent blend” of long and short hair. Castle felt “forced to admit *modification* of gametes from their original pure condition.” That is, the “paternal and maternal representatives of a character,” by virtue of their “union” within the germ, may “have exercised on each other a considerable influence.”<sup>451</sup> While he still accepted the basics of Mendelian genetics, Castle now rejected what had become a core doctrine that had major implications for evolutionary science.

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<sup>447</sup> William E. Castle, *Heredity of Coat Characters in Guinea-Pigs and Rabbits* (Carnegie Institution of Washington, 1905), 74, 76; Provine, *Sewall Wright and Evolutionary Biology*, 39.

<sup>448</sup> Castle, *Heredity of Coat Characters in Guinea-Pigs and Rabbits*, 66–67. For Castle, “latency” occurred when a trait, whether dominant or recessive, did not appear when expected, probably because it depended upon the existence of an additional independent trait. Working out epistatic interactions was one of Castle’s strengths and it is no surprise his student Sewall Wright emphasized them in his evolutionary theorizing.

<sup>449</sup> William Ernest Castle and Alexander Forbes, *Heredity of Hair-Length in Guinea-Pigs and Its Bearing on the Theory of Pure Gametes*, 49 (Carnegie Institution of Washington, 1906), 5.

<sup>450</sup> Provine notes that Davenport and Morgan had also questioned gametic purity, but they soon returned to a full commitment to the doctrine. Provine, *Sewall Wright and Evolutionary Biology*, 39.

<sup>451</sup> Castle and Forbes, *Heredity of Hair-Length in Guinea-Pigs and Its Bearing on the Theory of Pure Gametes*, 13. Note this all precedes the chromosomal theory of heredity and the discovery of crossing over. Castle’s theory was distinct from crossing over as well: crossing over is an exchange of genetic material between chromosomes, Castle was positing mutual influence.

Castle's interpretation of the new results forced him to modify his understanding of evolutionary dynamics. The degree of gametic contamination varied between traits which in turn determined the speed of fixation. In the case of ear length in rabbits, the genetic factors for short and long "completely blend and intermingle," allowing immediate fixation. In cases with complete dominance and segregation (traditional Mendelism as a special case) or when a character appeared only in the heterozygous state, contamination was minimized, thus requiring selection and inbreeding to fix.<sup>452</sup> Castle had flipped his evolutionary thinking from 1904 upside down: selection, natural or artificial, did not have to wait for mutations, but could actively produce new traits.

Castle's establishment of a true-breeding race of polydactylous guinea pigs also caused him to question his initial conclusions as presented in 1904: rather than a case of a sudden mutation *merely* "improved" by selection and breeding, the system was now evidence *for* selection's creativity.<sup>453</sup> In 1901, Castle had discovered a male guinea pig with an "imperfectly developed" fourth toe on one of its hindfeet. Although this pig's toe had a claw, the bones were unattached to the foot, hanging from the body like a "bag of skin," and fell off upon maturity. Seizing the opportunity, Castle bred the individual with a close relative. Within a few generations of inbreeding and selection, he increased the percentage of polydactylous offspring from 19.5% to 56%, some of which had a fully formed extra toe on each hind foot. By the fifth generation of inbreeding, Castle had produced a pair of polydactylous guinea pigs whose 88 offspring all inherited the trait.<sup>454</sup> Not only had Castle fixed the trait through inbreeding and selection, via gametic contamination, he had also changed ("improved") the trait itself: it appeared as if selection, not mutation, had been the major source of creativity. Although he, the breeder, had chanced upon a mutation, it was he who had transformed an imperfect toe in an individual into a full and fixed trait of a lineage. (See Figure 3.)

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<sup>452</sup> Castle and Forbes, 10. William E. Castle, "The Production and Fixation of New Breeds," *Proceedings of the American Breeders' Association* 3 (1907): 34–41.

<sup>453</sup> William Ernest Castle, *The Origin of a Polydactylous Race of Guinea-Pigs*, 49 (CIW, 1906).

<sup>454</sup> *Ibid.*, 27–28. Normally the species has four on its forefeet and only three on their hindfeet.

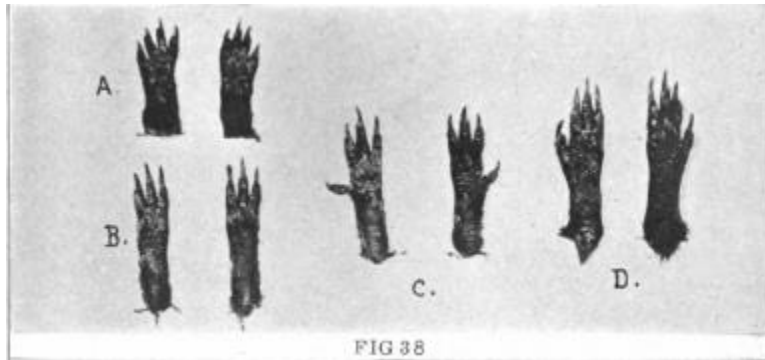


Figure 3: From Castle, *Heredity in Relation to Evolution and Animal Breeding* (1911), fig. 38.

Caption: "A. Front feet of an ordinary guinea-pig. B. Its hind feet. D. Hind feet of a race four-toed on all the feet.

C. Ordinary condition of the hind feet of a young [sic] obtained by crossing B with D."

Castle also claimed that Mendelism could not account for the trait's distribution in crosses. When he crossed a polydactylous pig with a normal pig, the offspring were neither uniform nor present in equal numbers (as expected in the  $F_1$  generation). When the experiment's middle generations were crossed, something like Mendelian ratios were sometimes given, but the *quality* of extra toes varied from "good" to "poor." That is, there was more than one dimension at play: discontinuous presence/absence *plus* continuous quality. The matter was too complex to fit into the simple framework of Mendelism. Thus, Castle interpreted the character's inheritance upon crossing with normal pigs as "intermediate between blending and alternative inheritance," in which "there occurs a *partial* blending of gametes in the zygote, and a *partial* segregation as the zygote gives off gametes."<sup>455</sup> Mendel's laws described only the extreme cases. And Mendelism as a special case had been revealed over the course of multigenerational experiments in which selection had played an active role.

Gametic contamination decided selection's precedence over mutation in breeding, enhancing the human control over evolution, although his still pluralist views maintained a role for mutation. Now believing that partial blending and segregation was the most common method of inheritance, "in dealing with such characters, selection must be the breeder's method of working." To overcome blending, the breeder had to carefully choose parents "many times over." But Castle did not relegate mutations to irrelevance. When it came to the extra toe's origin, Castle compared his results with those who

<sup>455</sup> Ibid., 24.

worked on poultry (Bateson) and humans (Davenport), concluding it arose by mutation, although not *de novo*. The extra digit appeared in the “precise position of a lost one” (in mammalian ancestry) along with “all the appropriate nervous and muscular connections,” so the extra toe must be *latent*, and thus appeared under certain and probably complex conditions. He concluded that while polydactyly and a “great many of the characters [that] distinguish ... domesticated animals and plants” originate as a “discontinuous character or mutation, ... without the aid of selection it would probably never become a racial character.”<sup>456</sup> Thus mutation retained an important role in revealing a latent trait or providing the germ for a new trait, but his experiments led him to turn towards selection as the major source of evolutionary creativity.

He wondered if “the same thing [was] true of a great many of the characters which serve to distinguish the various races of domesticated animals and plants?”<sup>457</sup> His question reflects a preoccupation with breeding and notably he did not extend it to nature. His theory as it was rested upon a mutation that became fixed through a process that overcame blending through choosing parents “many times over.” The relevance to nature was therefore unclear.

In his report to CIW, Castle regarded both the mutation and selection theories as “important in evolution.”<sup>458</sup> But because his interests were in breeding and control, a trajectory towards selectionism was not necessarily a surprise. Ironically, his new theoretical methods were more in line with that of the traditional breeder as artisan, rather than the “scientific” breeding that Castle had envisioned as emerging from Mendelism. Orthodox Mendelism could apply to special cases, such as coat color, in that it provided a “rational explanation of the origin of the various color varieties of rodent” via loss mutations, and it allowed the breeder predictable control of extant traits. But, it could not account for improvement (e.g., polydactyly) or blended traits (e.g., length of hair and ears in guinea pigs and rabbits, respectively).<sup>459</sup> Rather than mutation and Mendelism, Castle

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<sup>456</sup> Castle, 23–24, 29.

<sup>457</sup> Castle, 29.

<sup>458</sup> CIW Year Book, Vol. 5, 1906, p. 243.

<sup>459</sup> Castle also included a possible practical scenario for de Vries’ “mutation period,” but also demonstrates Castle’s distaste for waiting for them as a method: “It has been observed that one mutation is often followed by another. De Vries in his Mutationstheorie speaks repeatedly of periods of mutation. We can begin to see the significance of this; given one mutation, we can produce others. Suppose, for example, that we possess agouti and ordinary red varieties only and desire black, we are not compelled to await a

thought selection and gametic contamination were the keys to the control of evolution --- this not only emerged from his experimental work, but theoretically selection was evolution's most controllable force, opposed to waiting for mutations.

Although lop-eared rabbits and Angora and polydactylous guinea pigs had already begun to change Castle's views about evolution, the hooded rats clinched it. In 1907, Castle and MacCurdy reported to CIW the experiment's initial results, which reinforced selectionism and gametic contamination.<sup>460</sup> Because theories of evolutionary change are predicated upon theories of variation and inheritance, Castle now argued that gametic contamination overthrew the entirety of de Vries' thought.<sup>461</sup> Castle and MacCurdy considered de Vries to be "too sweeping" when he claimed that because continuous variation arose from non-inheritable environmental effects, that selection of extreme variations was incapable of permanently modifying a race. They argued that de Vries "overlooked" the possibility that not all causes of continuous variation need to be external. If *any* causes internal to the germ plasm acted to produce a continuous distribution, it should be inheritable, and such causes were not limited to spontaneous mutations. There was no logical reason to exclude germinal variations from being gradual, common, and accumulable. (Even his geneticist opponents, East and Shull, would agree, reflecting their pluralistic view.)

While Castle described the differences in theoretical terms, they clearly had implications for control. Under de Vries' theory, Castle claimed, "selection is unable to form new species, because it can neither call into existence mutations nor permanently modify a race by cumulation of abmodal fluctuations." Instead, selection could only

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mutation to produce it; we can cross red with agouti and obtain black in the second generation. ... To produce a red variety from agoutis and blacks alone would not be so easy; it would be necessary either to await a mutation or to work by the slow process of selection from continuous variations in the intensity of blacks under cross-breeding with agoutis." W. E. Castle, "On a Case of Reversion Induced by Cross-Breeding and Its Fixation," *Science* 25, no. 630 (1907): 151-53.

<sup>460</sup> Hansford MacCurdy and William Ernest Castle, *Selection and Cross-Breeding in Relation to the Inheritance of Coat-Pigments and Coat-Patterns in Rats and Guinea-Pigs*, 70 (Carnegie Institution of Washington, 1907).

<sup>461</sup> Specifically, de Vries' thought. Castle and MacCurdy did not engage with the emerging Mendelian-mutationism of Johannsen, Morgan, and Bateson. This explains Castle's conflation of continuous variation with fluctuation and large changes with mutation. The Mendelian-mutationists considered the degree of change and subsequent inheritance to be independent. Castle never abandoned this misconception of his opponents' views.



perpetuate extant variation and species. But,

Darwin, ... ascribe[d] evolutionary progress chiefly to the cumulation through long periods of time of slight individual differences. ... according to the Darwinian view, new species arise through the direct agency of selection, which leads to the cumulation of fluctuating variations of a particular sort.<sup>462</sup>

To test the two (somewhat outdated) alternatives, Castle and MacCurdy developed two new experimental systems — color patterns in hooded rats and in guinea pigs — to determine whether selection and inbreeding could “modify” discontinuous variations, specifically “to bridge the gap between them.” That is, could selection change the genetic factors themselves?

Their first new experimental system – and soon, major focus – was the manipulation of color distribution in the coats of hooded rats. The rats showed four different color distributions ranging from fully pigmented to “Irish,” hooded, and albino, each pattern a Mendelian dominant to the next. (See Figure 4.) Their intent was to select the stripe of the hooded rat to be wider and narrower to “bridge the gap” between these Mendelian alternatives. Bateson had asserted that these four patterns were “definite, and can not be built up by cumulative selection.” But Castle and MacCurdy, in fact, began to transform hooded rats towards both Irish and albino forms via selection and breeding. Castle reasserted that “heterozygosis leads inevitably” to gametic contamination, its degree corresponding to the “imperfection of dominance in the heterozygote.” In a special case of orthodox Mendelism, crosses between albino and pigmented rats produced “mixed litters ... close to the Mendelian expectations, indicating [no] selective union of gametes.”<sup>463</sup> This would prove to be an exception as the experimental system continued to demonstrate, according to Castle, creative selection and gametic contamination.

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<sup>462</sup> Ibid., 2–3. Castle to some extent misled his readership: While de Vries may have thought mutations created species, most Mendelians did not, as Castle himself had showed in 1904.

<sup>463</sup> MacCurdy and Castle, 7.



Figure 4: MacCurdy and Castle 1907, Plate I. The initial variation in the color pattern of the hooded rats, although not necessarily of the four types outlined by Castle.

Castle and MacCurdy began two long-lasting selection experiments — for wider stripes (“plus series”) and for narrower stripes (“minus series”). In the minus series, selection reduced the variability and “the distance between mean and mode,” implying that its effects “will be permanent” and that the new “variety will breed true.”<sup>464</sup> In the plus series, a bimodal curve initially resulted, interpreted as due *not* to the “heterogeneity of the material included” (which later became a common criticism), but indicated instead a

transitional condition, “that *part* of the gametes formed by the cross-bred individuals transmitted a modified (wide-striped) condition ... in process of segregation through the action of selection.” That is, they were witnessing the creation of a new gamete, catching selection in the act of creation. Indeed, propagating individuals from only the extreme end of the curve produced a generation whose stripes were all wider than the mode of the initial lot. There was no regression to the original mean. True also of the minus series, the curve was “nearly symmetrical, indicating approach to a condition of stability.”

Therefore, “characters can be permanently modified by selection.”<sup>465</sup>

The guinea pig experiment was similar: select from one extant character to another, “bridging the gap.” Like the rats, there were several common coat color distributions that

<sup>464</sup> MacCurdy and Castle, 15–16.

<sup>465</sup> MacCurdy and Castle, 17.

were alternative in inheritance: spots on the head, above the eyes, and on the torso. However, they could not “fix” these patterns as they could with the hooded rats; the trait was inherited only 50-80% of the time. What they did discover was that the *total* pigment was inherited and amenable to selection. They explained their apparently contradictory results — selection *for* head and rump spots or *against* shoulder spots both produced more spots overall — due to the varying rates in which pigment was dedicated to different areas; hence “the entire inefficiency of selection in guinea-pigs to fix a coat-pattern.” That is, after studying 1,048 pedigreed individuals, MacCurdy and Castle concluded that “one can by selection either increase or decrease the extent of the pigmented areas, but it is impossible by selection to fix this pigmentation in a particular pattern.” In this instance, “it is powerless.”<sup>466</sup> But, as Castle reported to CIW, “spotted races can be created at will which bear” either much or little pigment.<sup>467</sup> Clearly there were limits to evolutionary control by selection, but it remained the creative and controllable agency.

In their conclusion, MacCurdy and Castle suggested that de Vries’ own selection experiments with buttercups corroborated their experimental results — if only he had conducted them longer, he probably would have found regression decreased to a negligible degree. Combined with their own results, they asserted that “selection is a most important factor, not only in the isolation of discontinuous variations, but also in their production.” Furthermore, “a sharp line of division” could not be drawn between continuous and discontinuous variations (as well as between alternative and blending inheritance). Specifically, the distinct hooded and Irish patterns in rats followed Mendel’s laws, but Castle and MacCurdy had produced intermediates, “bridging the gap,” witnessing the origins of change in real-time. Thus, “it is fallacious to assign all evolutionary progress to one sort of variation or to one sort of inheritance.”<sup>468</sup> However, as their experiments continued, and despite the community’s move to the opposite pole regarding the creativity of selection, Castle would ignore this compromise in favor of selectionism. As Darwinism and Mendelian-mutationism separated, Castle affirmatively

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<sup>466</sup> MacCurdy and Castle, 19–27.

<sup>467</sup> CIW Year Book, Vol. 5, 1906, p. 243.

<sup>468</sup> *Ibid.*, 33–34.

supported “the Darwinian view” that selection was responsible for the establishment of new races, both natural and artificial, and was thus, the directive force of evolution.<sup>469</sup> For Castle, experimental evolution had re-established Darwinism.

### **George Shull and Edward East: From Darwin to de Vries and Johannsen**

George Harrison Shull and Edward Murray East integrated evolutionary science with plant breeding to articulate methods of control that had theoretical implications. By 1907, they adopted specific methods aligned with Mendel, de Vries, and Johannsen, as opposed to Darwinism and mass selection. Shull considered “mutation, Mendelism, and unit characters” to be “all part and parcel of one consistent view of the world of living matter.”<sup>470</sup> A view that not only described nature, but how to control it. Throughout this chapter I will present East and Shull as a pair, although they did not recognize their thorough agreement until 1908, having developed parallel views independently.

For both Shull and East, and like Castle, there was little that marked a difference between “pure science” and “practical breeding,” so long as that science was rooted in experimentation. As much as their work rejected Darwinian theories, they, like Bateson, recognized that a key to the Darwinian methodological tradition was experimental evolution; the “artificial” evolution in the field of maize or potatoes had as much to say about evolutionary dynamics as a population of flora and fauna in the wild. The role of experimental evolutionists, East envisioned, was to reduce the breeders’ “thousands of observations” and “surprising complications” to “a few natural laws.”<sup>471</sup> Their focus on practice aligned well with their positions at Agricultural Experiment Stations and the CIW-funded Station for Experimental Evolution.

To East, plant breeding was explicitly about the control and direction of crop growth and evolution, or in its capitalist guise: *improvement*. He differentiated farming practices along a spectrum of control: “beyond our control” were temperature and rainfall, “slightly under our control” were “attacks of insect enemies and parasitic fungi,”

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<sup>469</sup> MacCurdy and Castle, 3–4, 11.

<sup>470</sup> Shull, “Importance of the Mutation Theory in Practical Breeding,” *Journal of Heredity* 3, no. 1 (1907): 65.

<sup>471</sup> East, *The Relation of Certain Biological Principles to Plant Breeding*, 158 (Connecticut Agricultural Experiment Station, 1907), 5.

and “very largely under our control” were tillage, nutrition, and fertilization (although expensive). These environmental conditions (in addition to market fluctuations) contrasted with the control of heredity, “the productive forces which reside within the germ itself,” an area of still untapped potential.<sup>472</sup> As East wrote, “here are powerful factors in crop production ready to act for or against us, with or without our knowledge or control. It is the province of the corn breeder to obtain knowledge of and to bring these factors under his control.”<sup>473</sup> What exactly this control entailed was contested over the next decade.

There were numerous difficulties the plant breeder had to overcome that East argued animal breeders — more advanced, in his eyes — had not encountered. For one, much of animal breeding relied upon visible characteristics, such as coat color and size, whereas East was forced to develop methods to measure the chemical (protein and fat) content of maize kernels. More important, though, was that animal breeders dealt with mammals and birds with relatively stable sexually mating and reproductive systems, whereas plant breeders had to contend with an array of angiosperms with diverse mating systems. Maize, for instance, is wind-pollinated, and important developments in maize breeding were solely about controlling the mating process, especially detasseling and ear-to-row tests. The advantage plant breeders had, however, was high numbers.<sup>474</sup> Even though Castle would eventually pedigree over 30,000 individuals in his hooded rats experiment, this was dwarfed by the numbers Shull and East could produce. There were experimental virtues and costs to not only specific organisms, but the broad classes to which they belonged, namely animal and plant.

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<sup>472</sup> Interestingly, a search for “productive forces” in Google Scholar brings up mostly results from Marxist literature, East’s paper being the sole biological result. The related term, “productive powers,” comes from Adam Smith.

<sup>473</sup> East, *The Improvement of Corn in Connecticut*, Bulletin 152 (New Haven, Conn.: Connecticut Agricultural Experiment Station, 1906), 4. Breeding was not the primary focus of the agricultural experiment stations. East noted in 1908 that the most important problem in Connecticut agriculture was the productiveness of the soil and finding the best variety of crop for a particular soil type. East, “Report of the Agronomist,” in *Report of the Connecticut Agricultural Experiment Station for the Years 1907-1908* (Hartford, Conn.: State of Connecticut, 1908), 448.

<sup>474</sup> Another feature of maize is that its ears “must pass through the hands at husking time, and thus bring to notice its good and bad variations,” “undoubtedly [leading] to the conscious selection of the largest ears for seed from very early times, and has given to us many types of greater or less excellence.” East, *The Improvement of Corn in Connecticut*, 5–6. This is another example of Darwin’s “incrementum” and “metonymy” discussed in Chapter 1.

East's career began with an important long-term selection experiment of maize at the Illinois Agricultural Experiment Station. The experiment's goal was to increase a kernel of maize's protein or oil content at will. The work was quite thorough, analyzing maize's microscopic structure and pointing to practical ways the ordinary farmer may improve his crop by his own artificial selection.<sup>475</sup> As much as historians have emphasized the experiment's relationship to the problem of selection, Hopkins, Smith, and East considered the "most important improvement" to be "that which relates to the prevention of inbreeding."<sup>476</sup> Indeed, they were *explicitly* Darwinian, attributing (partially) to him the "well-known principle ... that injurious effects are produced from the self-pollination of plants which are naturally cross-pollinated."<sup>477</sup> That is, inbreeding produced "evil effects." At this point in 1903 East remained Darwinian, regarding both inbreeding and the effects of selection, but in a reverse example to Castle, he later reinterpreted these results along Mendelian-mutationist lines alongside practical and theoretical developments. Like Castle, the longer the experiment continued, the more he was convinced his initial position was incorrect. These two are a rich demonstration of Bukharin's interplay of practice and theory with the former leading but not determining the latter.

East and Shull embraced the theories of de Vries, although they did not accept it entirely. East was skeptical of the *Oenothera* work, for example, but believed that "other data by Bateson, De Vries, and others, [were] more convincing to my mind."<sup>478</sup> There

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<sup>475</sup> Cyril G. Hopkins, East, and Louie Henrie Smith, *The Structure of the Corn Kernel and the Composition of Its Different Parts*, 87 (Urbana, Ill.: University of Illinois Agricultural Experiment Station, 1903).

<sup>476</sup> Cyril G. Hopkins, East, and Louie Henrie Smith, "Directions for the Breeding of Corn, Including Methods for the Prevention of in-Breeding," *Bulletin (University of Illinois (Urbana-Champaign Campus). Agricultural Experiment Station)*; No. 100, 1905, 601. Shull at this time also noted the importance of isolation [Prob out of place] and progeny tests as developed by Vilmorin, Willet Hays and Hjalmar Nilsson. Shull, "Importance of the Mutation Theory in Practical Breeding," 64.

<sup>477</sup> Hopkins, East, and Smith, "Directions for the Breeding of Corn, Including Methods for the Prevention of In-Breeding," 602.

<sup>478</sup> East, *The Relation of Certain Biological Principles to Plant Breeding*, 34. East addressed this again in 1914, writing that although "de Vries did indeed lay great stress upon his work with the evening primroses," he produced additional "props so sturdy that in the opinion of some, the *Oenothera* investigations might be disregarded without weakening the edifice. East, review of *The Mutation Factor in Evolution: with Particular Reference to Oenothera*, by Reginald Ruggles Gates, *Rhodora* 17, no. 204 (1915): 235. That is, historians' tendency to treat the mutation theory as wholly dependent on the success or failure of *Oenothera* is misguided. However, East implied that de Vries' mutation theory was "no new Evolution theory." De Vries "showed the frequency with which germinal changes of comparatively great size occur, and why they are not swamped by intercrossing. [These] merely extend and modify Darwin's ideas insofar as these new facts tend to change the emphasis the latter placed upon particular types of

were numerous breeding examples de Vries could have cited instead, such as the little red poppy (*Papaver rhæas*), a long neglected plant that suddenly produced a remarkable individual in 1882 that the English Reverend Wilks isolated, transplanted, and propagated, resulting in the Shirley poppy.<sup>479</sup> Therefore, the popularity that the mutation theory enjoyed in the United States did not rest solely upon *Oenothera*; as Shull stated, signaling the importance of practice, “even its most strenuous opponents grant that it is supported by garden experience.”<sup>480</sup>

Of utmost importance to understanding the entire debate that followed was *the distinction, first made by de Vries, between “fluctuations” and “mutations.”* (This was explained in Chapter 2.) East and Shull repeatedly pointed to this distinction as his greatest contribution: a scientific explanation for breeders’ mixed experiences with mass selection. As East and Shull recognized, de Vries distinguished between fluctuations: environmentally caused, temporarily inherited, linear variation; and mutations: internally caused, permanently inherited, discontinuous and definite variation in any direction. The implication of this distinction, theoretically and practically, was that much of the visible variation within a population was not inheritable and, therefore, not selectable. (It also pointed to a rejection of the inheritance of acquired characters.) Although historians, as well as opponents such as Castle, tend to equate mutations with large-scale variations and fluctuations with small-scale variations, the distinction was actually one about inheritability and response to selection. Shull admitted that known mutations tend to be “large and striking,” but this was a result of an expected bias of breeders to simply notice them more frequently.<sup>481</sup> East was more explicit, stating that “the mutation may be within the limits of a fluctuation, but still be a true mutation.” (Indeed, there is no other way for Johanssen’s experiment to have made any sense.) According to Shull, what characterized a mutation was a “fundamental [and “transmissible”] change in the internal composition or structure of the vital substances”; mutations are “often very insignificant,

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variation” (p. 235). This passage signals a synthetic view of evolution independent of the more “ideological” scientists, such as Bateson or Pearson, but bears more in common with Mendelian-mutationism.

<sup>479</sup> Shull, “Importance of the Mutation Theory in Practical Breeding,” 62.

<sup>480</sup> Shull, 65.

<sup>481</sup> Shull, 62. Therefore, the Morgan lab’s accomplishment regarding mutations was not proving that they were small, for this was already accepted; instead, their accomplishment was to build an experimental system to better detect and understand mutations, à la Robert Kohler’s notion of the “breeder reactor.”

quantitatively.”<sup>482</sup> This distinction was the central theory that animated a decade of debate among the experimental evolutionists.

The careful methods East developed were precisely because “fluctuations overlap and are indistinguishable in appearance.” (The difference “is merely in their transmission.”)<sup>483</sup> For example, a pure line of sugar beets may normally produce 12% sugar with fluctuations between 10-14%, whereas another line may normally produce 10% sugar with fluctuations between 8-12%. East’s and Shull’s methodological goal was to differentiate between these two lines via pedigree breeding.<sup>484</sup> In addition, a mutation produced “a new range of fluctuating variability,” possibly with a greater range than the parents. Because of this overlap, recognizing and accounting for the problem would increase the efficiency of crop improvement.<sup>485</sup> This meant that this theoretical distinction that emerged from practice was a distinction that could be made only by practice in any given situation.

East and Shull considered this a non-Darwinian, if not anti-Darwinian, view of evolution, but this did not entail a rejection of selection. As East explained (and citing Morgan),

... Natural selection theory is mainly ... a theory of adaptation to environment. It is a sieve which sifts out variations which have appeared that are of prime utility to the organism or to the species. It is not a cause of evolution itself, but a working agent for destroying organisms less fit for their station in life than some of their relatives or species less fit for existence than others. It is not a selective agency, but a rejective agency. It is plainly evident that it is one of the great factors of evolution, possibly the greatest factor; but it is as plainly evident, even with the added theory of sexual selection, that numerous characters possessed by living organisms must have developed without its agency.<sup>486</sup>

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<sup>482</sup> Furthermore, bud variations and hybrids were not mutations. This distinction he considered one of the most practical benefits of the theory. Shull, 61, 65.

<sup>483</sup> East, *The Relation of Certain Biological Principles to Plant Breeding*, 35. East repeated this interpretation numerous times: East, *A Study of the Factors Influencing the Improvement of the Potato*, 127 (Urbana, Ill.: University of Illinois Agricultural Experiment Station, 1908), 417; East, review of *Principles of Breeding*, by E. Davenport, *Science* 29, no. 737 (1909): 261–62. See also: East, “The Role of Selection in Plant Breeding,” *Popular Science Monthly* 77 (1910).

<sup>484</sup> East, *The Relation of Certain Biological Principles to Plant Breeding*, 35.

<sup>485</sup> Shull, “Importance of the Mutation Theory in Practical Breeding,” 66. At this time, East and Shull accepted de Vries’ contention that selection could act upon fluctuations, but only temporarily, and they soon discarded this, taking a hardline position that fluctuations were by definition not inheritable.

<sup>486</sup> East, *The Relation of Certain Biological Principles to Plant Breeding*, 23–24. The last sentence partially refers to the Duke of Argyll’s criticism that natural selection cannot explain the origins of traits because they could not have been adaptive in rudimentary form. (Another criticism that East took to heart was



This quotation, and East's work in general, undermines the literature's emphasis on "anti-" or "non-Darwinians" rejecting selection. As East himself states, selection, although non-creative, and even non-causal, is "possibly the greatest factor in evolution." Selection's importance in evolution contradicted its lack of importance as a source of creativity.<sup>487</sup>

East's 1909 review of Eugene Davenport's *Principles of Breeding* reveals the confusion and differences between the two standpoints. (No relation to Charles Davenport.) First, according to East, Davenport promulgated the "false impressions among out and out Darwinians" who "seem to be able to conceive a mutation only as the addition or loss of a complete character and therefore a wide jump." But East pointed out that mutations were mostly "quantitative changes in characters already possessed, i.e., simply the production of new modes as centers for linear fluctuation. The difference between fluctuations and mutations is merely in their transmission."<sup>488</sup> (Davenport accepted East's correction, redefining them along Mendelian-mutationist lines.) As for selection, East described Davenport's "biometrical explanation" as "explain[ing] nothing." Davenport argued that "the principal function of selection ... is to *alter the type, not to reduce variability*"; fixing the type was therefore impossible because "there always remains sufficient variability for further selection." East rejected this view: selection altered the type *by* reducing variability, i.e., by eliminating alternative types from a heterogeneous mixture. According to East, this was a "real explanation compatible with the belief that to be inherited variations must have affected the germ cell structurally — a view to which the author [Davenport] adheres." That is, Eugene Davenport's selection theory was tied to Pearson's "lame biology," based on statistics and ignoring underlying causes and mechanics, rather than to his own Mendelism.<sup>489</sup>

For East and Shull, the question in terms of practice was not whether to abandon "selection," but *what kind of selection* was most efficient — "Darwinian" mass selection

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Kelvin's age of the earth argument.)

<sup>487</sup> While I am making use of dialectical materialism to analyze the historical developments, the theory proposed by East here is *not* dialectical but is instead one-sided: Levins and Lewontin, for example, would point to niche construction as undermining the mechanical sieve metaphor.

<sup>488</sup> East, "Principles of Breeding," 261–62.

<sup>489</sup> East, 262–63.

of fluctuations or “de Vriesian” individual selection between pure lines originated by mutation. But, East noticed, the theoretical disputes over evolution were simultaneously of “primary and direct importance to plant breeding ... for the factors [variation, heredity, selection] in the improvement in crops are the same as those of a natural evolution.”<sup>490</sup>

Shull agreed with the identity of nature and artifice in this case, writing that,

If the mutation theory holds for plants and animals in a state of nature, and this appears daily the more probable, then mutation is the basis for the origin of every permanent variety or strain. In nature, mutations have been preserved because they were adapted to the life conditions in which they originated; in the garden they have been preserved because they pleased the eye of man or promised to minister to his wants or needs.<sup>491</sup>

East’s rejection of Darwinism (not selection) initially seems incongruent with his experience at Illinois, but to the contrary, East now believed de Vries and Johannsen better explained the results. The Illinois maize experiment had made rapid progress in increasing and decreasing protein and fat content, but was approaching a limit. A corroborating scenario was that of beets, in which selection had not improved sugar content over the past thirty years, but had prevented deterioration from crossing. That is, “the isolation of the pure lines is fast being accomplished,” although its permanence, predicted by Johannsen, remained undetermined.<sup>492</sup>

East explained the evolutionary dynamics of the situation as follows. Whether a Darwinian (mass) or de Vriesian (pedigree) method of selection was followed, its tendency was to sort between and isolate types within the field. Where they differed was in the rate, due to two major factors. First, uncontrolled crossing under mass selection produced heterogeneity (soon labeled heterozygosity), a “mixture of several types” that contained within them “‘blood’ of types less productive. ... By continuous and very rigid selection we will necessarily reduce the number of types.” Second, fluctuations produced by environmental effects, such as non-uniform soil conditions, could make a less productive type overlap with a more productive type, propagating it to the next

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<sup>490</sup> East, *The Relation of Certain Biological Principles to Plant Breeding*, 19.

<sup>491</sup> Shull, “Importance of the Mutation Theory in Practical Breeding,” 62.

<sup>492</sup> East, *The Relation of Certain Biological Principles to Plant Breeding*, 46–47. East also recognized the relationship of population size in this context — the higher the number of individuals, the more likely an extreme fluctuation was to appear, thus lessening the need for improvement via selection. This would become important when East developed the multiple factor theory.

generation despite its genetic inferiority. This explained a population's initial and rapid response to mass selection, as well as its eventual halt and, if selection were discontinued, the population's regression. Thus, de Vries, Pearson(!), Johannsen, "and the experience of breeders" in general contradicted "the opinion of Darwin that by selection the type of the race would be raised and a new selection possible from the extremes in fluctuation of this new type." Rather, there was a "limit to the amount of improvement that could be made."<sup>493</sup> East had carefully distinguished between two types of selection and had worked out their practical implications.

Shull reached the same conclusions: "contrary to the general belief of breeders," Darwinian mass selection was inferior to "the method of isolation of types by pedigree cultures" worked out by Vilmorin, Hays, and Nilsson and scientifically developed by Johannsen – a theory condensed from practice. Johannsen's theory held that isolating a pure line produced a strain that would breed true to its type, rather than regressing to the original mean. (This was the theoretical basis of Shull's development of hybrid corn discussed below.) Shull explained the "characteristic features of the method" to be "the production of enormous numbers from which to select, the complete isolation of each individual whose characters suggest the possibility that it may be the starting point of a new strain, the complete control of the fertilization processes, and the rearing of the offspring of the guarded plants under conditions that will allow all distinguishing characteristics to reach a normal development."<sup>494</sup> The point was to *control against* contamination, crossing, regression, and inbreeding. (The worry over inbreeding, a holdover from Darwin, was the next major problem tackled by Shull and East, discussed below). But bringing a crop under such a degree of control may have made extrapolations to nature tougher than before; after all, detasseling does not occur naturally.

Despite their emphasis on production and control, both noted the method's passivity. East wrote, "in no case are we trying to force a variation along unnatural lines;

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<sup>493</sup> East, *The Relation of Certain Biological Principles to Plant Breeding*, 29–30. With respect to Pearson, East saw little conflict between biometry and what would become genetics. He thought the law of ancestral heredity "approximate[d] the truth" when applied to a whole organism with thousands of characters or when dealing with the averages of a population, but it failed to work for individual characters and could not describe the results of individual crosses or the physiology of heredity. Why East saw Pearson as aligned with de Vries and Johannsen he left unclear. East, 28, 44.

<sup>494</sup> Shull, "Importance of the Mutation Theory in Practical Breeding," 66.

we take types as nature has produced them, isolate, propagate and use them. In most crops there is no need for selection other than to obtain the necessary purity of type.”<sup>495</sup> Shull “confidently expected” that mutations could soon be artificially induced — not only in terms of frequency, but perhaps even their direction. MacDougal’s injection experiments pointed to the possibility, but “we seem to be at present entirely *at the mercy of nature*.”<sup>496</sup> But, now that biologists had developed a new theory about how evolution worked in nature and in the garden, “nature treats us well, if we stand equipped with as complete understanding of her ways as science provides, *ready to take advantage of and preserve every advance she makes*.”<sup>497</sup>

East and Shull concluded that selection could maintain a race, but not create it, contrary to Castle’s recent views. Selecting fluctuations may prevent deterioration and regression, but “this is entirely distinct from trying to breed into a variety by selection a heritable character that it does not naturally possess.”<sup>498</sup> The difference between “selection” and “isolation” was blurry, since the former “does contribute toward the slow isolation of the best natural high yielding type,” but the theoretical underpinning was quite different. Thus, while passive, it was more efficient; Shull estimated that the successful development of a new strain of barley through mass selection over twenty years could have been accomplished through isolation in five years.<sup>499</sup> Creativity was left for nature itself, while selection was within the hands of breeders. This contrasted with Castle, who was now arguing that creativity *and* control were identical with selection.

It cannot be forgotten that a crucial third method of plant improvement enjoyed a long history — hybridization — and had received a recent boon from Mendel. While East considered the belief that “Mendel’s work will make the characters of hybrids as easy to predict as are those of chemical compounds” to be “an extreme view,” Mendel did provide “the most direct plan of procedure in combining known desirable characters possessed by distinct varieties,” once the characters were confirmed to Mendelize. (This

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<sup>495</sup> East, *The Relation of Certain Biological Principles to Plant Breeding*, 55–56.

<sup>496</sup> Emphasis mine. Sharon Kingsland discusses MacDougal extensively in “The Battling Botanist: Daniel Trembly MacDougal, Mutation Theory, and the Rise of Experimental Evolutionary Biology in America, 1900–1912,” *Isis* 82, no. 3 (1991): 479–509.

<sup>497</sup> Shull, “Importance of the Mutation Theory in Practical Breeding,” 66. Emphasis mine.

<sup>498</sup> East, *The Relation of Certain Biological Principles to Plant Breeding*, 59.

<sup>499</sup> Shull, “Importance of the Mutation Theory in Practical Breeding,” 63.

was Castle's position prior to supporting gametic contamination.) According to East, Mendel additionally "brought confirmatory evidence that characters are established fully formed by mutation, and are inherited as such."<sup>500</sup> In terms of practice, though, East advised isolation should be done prior to any hybridizing, since "at present it is undesirable to complicate the work until we have accomplished what can be done without it."<sup>501</sup> As mentioned above, Shull also embraced Mendelism, but in the context of plant breeding, he, too, did not place much emphasis upon it, at least at the time, for he would soon develop a method of hybridizing maize with known genetically inbred strains.

East concluded, acknowledging the "pronounced De Vriesian view" he presented, that

the view is from the standpoint of the principles and theories that give at present the most practical and efficient help in actual plant breeding. ... It may be admitted that certain forces may have been of great value in effecting an evolution through eons of time, and [yet] still be ineffective agents in the time allotted to the man who wishes to make changes under domestication from the standpoint of commercial gain. It is here that the two lines [philosophical and experimental biology] part company; and it is the plant breeder who remembers this distinction between natural and artificial evolution when studying disputed theories of variation and heredity, that will obtain the greatest aid from the results of the experimental biologist. We may admit, for instance, that the believer in Lamarckian factors as agents in evolution can say that experiments concerning the inheritance of acquired characters have been carried on only for a period of time that would be negligible in a geological epoch; we may admit the justness of the same criticism of our conclusions regarding the ineffectiveness of the selection of fluctuations in permanently changing characters: but we are justified in retorting that only such theories can be of use to us that produce results within the span of a human life.<sup>502</sup>

Thus, East's primary concern with breeding practices and experimentation, primarily time, motivated his theoretical understanding of evolution. He alluded to potential differences between nature and artifice but had played it down due to its experimental intractability (time). This introduced an interesting notion that the process of controlling

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<sup>500</sup> This relies on an assumption that a tall or short allele and morph in peas, for example, were formed as such and not evolved over time.

<sup>501</sup> East, *The Relation of Certain Biological Principles to Plant Breeding*, 64–72, 79–80.

<sup>502</sup> East, 90. The rhetorical device of comparing what happens in nature and what humans do is common in East's and Shull's writings.

evolution differed from its natural method, despite being based on the same causes, laws, and material.

Shull, for his part, admitted that it was possible that “old methods” of breeding may “harmonize perfectly with the theory,” relegating the mutation theory’s practical significance to “better appreciation” of what breeders already grasped.<sup>503</sup> For example, dissolving the boundary between nature and artifice, “sports or mutants are [now] recognized as normal products of a natural process,” and their usual minuteness forced the breeder to pay closer attention for inherited differences than they formerly would have.<sup>504</sup> But Shull also believed there was a larger spiritual significance:

... The value of the mutation theory is great in the feeling it gives the breeder that he is handling the normal and eternal forces of nature. An added interest attaches to each new variation when it is realized that every instance of mutation is a part of the order or [sic] nature, and not a monstrous departure from natural conditions; and the sense of exaltation that comes from dealing with the processes and products of universal evolution cannot fail to increase enthusiasm and efficiency in the breeder’s work.<sup>505</sup>

But, the most significant development, beyond naturalizing mutations and explaining existing practices, was their landmark work on hybrid maize. This not only contributed to the United States’ future skyrocketing corn production, but also shaped evolutionary theory. Until now, they had conducted most of their work without much reference to genetics, hence their work being properly considered experimental evolution, but this would change as they found it to be useful explanatorily.

### **Shull's Development of Hybrid Corn and Overturning the Anti-Inbreeding Bias**

Still the Station for Experimental Evolution’s botanist, Shull conducted breeding experiments with maize that reshaped the biological view of inbreeding and its value. This was largely due to the incorporation of genetics into pure line and mutation theories

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<sup>503</sup> This claim falls in line with the historical consensus that genetics itself did little to improve techniques, but instead explained them scientifically. I discuss this issue elsewhere. However, even at this point, later known for their genetics work, both East and Shull were not incorporating Mendelism into their theories yet — their work is primarily under the influence of de Vries, Johannsen, and the late 19th C. Breeders Vilmorin, Hays, Nilsson.

<sup>504</sup> Shull, “Importance of the Mutation Theory in Practical Breeding,” 63.

<sup>505</sup> Shull, 66–67. Although the degree that a non-scientist breeder would feel this way is uncertain.

that Shull had so far helped develop. From that work he would help develop hybrid corn, an important agricultural feat, and perhaps the most important practical innovation from this era of experimental evolution. Typically considered an innovation in agriculture or genetics, I argue that hybrid corn is more properly an accomplishment of experimental evolution, despite Shull's acknowledgement that the work had little to say about how evolution occurred in the wild, representing a further distinctly artificial trend within the tradition. Furthermore, this work was the reverse case of Darwin's theorizing: Darwin took artifice to stand in for nature, whereas Shull and East moved from nature to artifice. This difference was also reflected in the ties to capitalism: While both Darwin's "experiment on a gigantic scale" and hybrid maize were the result of capitalist developments, Darwin had also tied his work into the rich "entangled bank" of natural history; the intention of hybrid maize was the reductionist control of a commodity's evolution for profit. Thus experimental evolution contained the possibility of escaping the constraints of natural evolution, but was not defined by it.

Interestingly, though, Shull acknowledged this contradiction but rejected it somewhat. Shull's research on maize rested primarily upon pedigree culture, the "peculiar instrument" of genetics. Well-aware of potential limits of artificial work, he acknowledged that methodologically "the distinctive feature ... [of] isolation [is] unlike anything which commonly occurs in nature," its results having "valid application only to those rare situations in which similar isolation is found in nature." Shull countered, however, arguing that its distinctive feature was not isolation, "but perfect knowledge of ancestry."<sup>506</sup> He added, citing de Vries' extensive *Oenothera* pedigrees,

It is needless to urge that in nature no other than the possible combinations exist, and that therefore when with respect to any species or group the full scope of the pedigree-method has been utilized we have the fundamental data upon which alone can be based any proper conception of what goes on in nature, and that the data so found when properly confirmed by repetition are applicable to all nature in which the particular species or group in question is involved.<sup>507</sup>

Thus, Shull argued that through artifice, the scientist could work out all possible

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<sup>506</sup> George H. Shull, "The Pedigree-Culture: Its Aims and Methods," *The Plant World* 11, no. 2 (1908): 21–22.

<sup>507</sup> Shull, 22.

combinations and this knowledge allowed one to extrapolate experimental results back to nature. Like Mendel, Shull bridged the gap between laboratory and nature by working with “the composition of a field of maize.”<sup>508</sup>

So far, maize had proved to be exempt from improvement by pure line methods. Although he had himself praised the power of isolation methods in crop improvement, self-fertilized maize tended to deteriorate. This lent credence to the belief that inbreeding produced “evil effects,” or in more scientific language, that it resulted in the “inharmonious or unbalanced constitution produced by the accumulation of disadvantageous individual variations.” But, given pure line theory’s success elsewhere, these old explanations were becoming insufficient.<sup>509</sup> Shull thus set out to work out how maize could be incorporated into the emerging theories of variation, heredity, and evolution.

Shull’s work on maize was an extension of Johannsen’s. Shull replicated Johannsen’s experimental design by planting the offspring of self-fertilized ears of corn along rows. When cultivated, differences between the rows were “immediately apparent,” including height, stalk diameter, leaf color, susceptibility to fungus, and the number of rows in an ear.. And typical of F<sub>1</sub> hybrids, rows of cross-bred ears resembled one another. The differences between self-fertilized rows were hereditary, thus constituting, in Shull’s view, “elementary species” or “biotypes” à la the mutation theory. Because Shull tested traits beyond height or weight, such as vigor, he was able to conclude that self-fertilization did not result in deterioration; instead, self-fertilization isolated types of varying qualities. Inbreeding’s effect was indirect and “simply isolated the two [biotypes] by separating them from their hybrid combinations with other elementary species.” Inbreeding could not be the “direct cause” of deterioration.<sup>510</sup>

True to de Vries and Johannsen, Shull explained that what frequently appeared to be variations within a self-fertilized line of maize were impermanent. Instead, a biotype varied about an inherited mode.<sup>511</sup> The character of a biotype’s offspring sat between the

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<sup>508</sup> George H. Shull, “The Composition of a Field of Maize,” 1908.

<sup>509</sup> Shull, 296.

<sup>510</sup> Shull, 297–98.

<sup>511</sup> Shull still thought selection could “temporarily modify” a biotype, but regression would take hold as soon as it ceased or the conditions changed.



parents and the mode, but selection could reduce the discrepancy, i.e., variability. Selection could also “detect” biotypes from a mixture through isolation, such as when Shull found a 10-rowed stock among one that averaged 12-14 rows.<sup>512</sup> This was much like how Johannsen’s beans had displayed a normal curve of variation in terms of weight, but they were actually a population of distinct types.

From these experiments, Shull concluded the “obvious”:

An ordinary cornfield is a series of very complex hybrids produced by the combination of numerous elementary species. Self-fertilization soon eliminates the hybrid elements and reduces the strain to its elementary components. In the comparison between a self-fertilized strain and a cross-fertilized strain of the same origin, we are not dealing, then, with the effects of cross and self-fertilization as such, but with the relative vigor of biotypes and their hybrids.<sup>513</sup>

Shull thus explained that within a field of maize were numerous, hidden biotypes, themselves disguised within hybrid combinations. While Shull was not advocating a modern populational view, it was not a purely “typological” view either. Contrary to Ernst Mayr’s strict dichotomy, the pure line theory appears to be a transition in “population thinking.”<sup>514</sup> These scientists were working out the implications of mutationism and Mendelism on populations, or in this case, “the composition of a field of maize.”

In practical terms, self-fertilization broke the hybrids into their constituent biotypes. Due to Mendelism, a hybrid cross could also reveal the biotype in the homozygotic class, but only if the offspring were from two “rigidly selected” parents. It

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<sup>512</sup> Shull, 298–99. Shull added, “the greater vigor of the cross-fertilized rows is thus immediately brought into harmony with the almost universal observation that hybrids between nearly related forms are more vigorous than either parent.” That is, cross-fertilization and hybridization were both a merging of two types.

<sup>513</sup> Shull, 299.

<sup>514</sup> For additional evidence of this transition, see Shull, “Elementary Species and Hybrids of *Bursa*,” *Science* 25, no. 641 (1907): 590-591; Shull, *Bursa bursa-pastoris and Bursa heegeri biotypes and hybrids* (Washington, D.C.: Carnegie Institution of Washington, 1909). In his study of the highly variable shepherd’s purse, Shull determined that there were at least four “biotypes” or elementary species within the Linnean species that required pedigree culture to identify. He showed these biotypes Mendelize, their differences consisting mainly of two unit-characters, but claimed that when hybridized, they re-emerged in full in the F<sub>2</sub> generation (i.e., did not break apart and recombine as would become the dominant theory. Thus, while Shull’s notion of biotypes is outdated, he was also finding the precise ways in which a species contains genetic variation. Shull also at this time suggested that recessive biotypes benefited from being able to hide within hybrids and speculated on how this scenario would play out in nature.

would be “much slower” to work, however, because of the “reintroduction [of] elements” eliminated in the father strain from the mother strain, and vice versa.<sup>515</sup> Interestingly, Shull still maintained a distinction in his analysis between pure line theory and Mendelism.

Shull inverted the practical problem regarding maize: it was no longer the prevention of inbreeding, but the “development and maintenance of that *hybrid combination* which possesses the greatest vigor.” While selection would initially improve the strain by eliminating maladaptive “components,” if it “continued in the same rigid manner” “it may lead to the loss of one after another of the component biotypes” that produced the desired vigor. Shull concluded, therefore, that “the fundamental defect in every empirical scheme of corn-breeding” based in isolation “lies in the fact that there is no intelligent attempt in these methods to determine the relative value of the several biotypes *in hybrid combination*, but only in the pure state.”<sup>516</sup> It was impossible, however, to predict the vigor of a cross between two biotypes. Pointing to the methods of a hog breeder who crossed two original strains every year to remake the same hybrid, Shull suggested the same for corn breeders (which proved to be adopted method). He also suggested carrying out selection “to a point at which the most efficient combination has been isolated from the less efficient components” and then “relaxed” so as to not eliminate the constitutive biotypes. Here Shull began to point to another function of selection in addition to isolation: the maintenance or even *creation* of hybrid combination.

### Shull's and East's Consolidation

Once East and Shull became aware of their shared understanding of evolution and plant breeding, their views became even more integrated and consolidated, particularly with respect to inbreeding and maize. In his report as station agronomist, East picked up on Shull's new theory and technique of inbreeding. Explaining again the work of de Vries and Johannsen, East noted that his previous bulletin had advised methods based in a “fear

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<sup>515</sup> Shull, 299–300. How exactly he saw this working is unclear, given that the paper predates the discovery of crossing over.

<sup>516</sup> Shull, 300.

of the dangers of inbreeding,” a belief rooted in Darwin’s work as well as his own experiences with maize.<sup>517</sup> Now, East believed Shull had “given ... the correct interpretation of this vexed question”: “instead of saying there is a loss of vigor through inbreeding, we say there is an increase in vigor from hybridizing.” In a bulletin he declared the method to be “worthy of trial.”<sup>518</sup>

However, “with the conception of biotypes within a species, there is a radical change in the thought.” East deduced from Shull’s hypothesis that because of the relationship between inbreeding and degeneration, there should be a limit to degeneration. Now more fully integrating Mendelism into their work, East suggested degeneration would end upon reaching homozygosity, i.e., genetic uniformity.<sup>519</sup>

With the new theory, East reevaluated Darwin’s *The Effects of Cross and Self Fertilisation in the Vegetable Kingdom* (1876), discovering that Darwin’s experiments corroborated Shull, despite Darwin having reached a contradictory conclusion. Specifically, when comparing self-fertilized lines, Darwin assumed that inbreeding necessarily had a negative and degenerative effect, but Shull and East now argued that isolated/inbred biotypes may vary in quality.<sup>520</sup> East picked out a ten-generation experiment with *Ipomea purpurea*, in which Darwin compared heights of crossed with selfed lines, and instead of the latter continually decreasing in height, they began to converge to a limit.<sup>521</sup> The flower color of the selfed lines varied less than in the crossed lines, enough so that Darwin’s gardener could identify a type by the trait alone, with no sense of “deterioration,” i.e., Darwin had actually isolated biotypes.<sup>522</sup> East argued that when reconsidered in new light, Darwin’s experiments were actually “in strict accord with the modern theory” which stated that “with continued inbreeding there is no

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<sup>517</sup> East, “Report of the Agronomist,” 421–22.

<sup>518</sup> East, 422, 428.

<sup>519</sup> East, “Report of the Agronomist,” 423.

<sup>520</sup> East, 424.

<sup>521</sup> Darwin measured height as the selective index, whereas Shull and East used multiple characters, but especially yield. East was skeptical of the utility of height, choosing to measure fecundity. [Make sure true:] This choice was what produced the different conclusions.

<sup>522</sup> Another experiment of Darwin’s with *Petunia violacea* lasted five generations, and while there was overall deterioration, the third selfed generation was more vigorous than the crossed. As he put it later, “Darwin was not dealing with the same strain at the end of his experiments that he was at the beginning.” East and H. K. Hayes, *Heterozygosis in Evolution and in Plant Breeding*, vol. 243 (Washington, D. C.: Bureau of Plant Industry, 1912), 16.

accumulation of detrimental characters.”<sup>523</sup> Instead, “this change was due ... to the elimination of Mendelian segregates.”<sup>524</sup>

Already having reinterpreted the Illinois maize experiment in light of the mutation theory, East addressed it once again, but now with regard to Shull’s hypothesis.<sup>525</sup> While the experiment had initially shown that “inbreeding in corn was deleterious to its vigor,” it now indicated that the “superiority of crossed over inbred seed was not on the increase.” He predicted that “continued selection will also, though more slowly, isolate a uniform type upon the crossed rows, which will bring the yields of tasseled [inbred to varying degrees] and detasseled [crossed] closer together.”<sup>526</sup> That is, both self-fertilization and mass selection theoretically reduced variability, but at different rates, with different degrees of control, and ended with different products: a biotype versus the best hybrid combination.<sup>527</sup> Like fluctuation and mutation, East was identifying operational and practical differences among apparently identical phenomena.

The role of environmental action in creating fluctuations that could mask discrete pure lines or mutations remained important to these investigations. To examine the question, East turned to the potato, a crop with few breeders working on its systematic improvement. East asserted that “there are characteristic differences in seeding power which are inherited by different varieties. Fluctuations in these characters are so large and may be increased artificially by changing environmental conditions; but no ordinary treatment will force a variety across its critical point into another biotype.”<sup>528</sup> After analyzing the hereditary and environmental factors that influenced potato and tuber development, East wrote that:

Our whole problem is reduced to the question whether types may or may not be changed by the selection of fluctuations. If types may be changed by the selection of individual fluctuations, they may likewise be changed by the selection of partial fluctuations. Until recently an affirmative answer to this theorem would not have been questioned. All of our conclusions, however, have been based upon the supposition that the data obtained in

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<sup>523</sup> East, “Report of the Agronomist,” 425.

<sup>524</sup> East and Hayes, *Heterozygosis in Evolution and in Plant Breeding*, 243:16.

<sup>525</sup> Should I reiterate what East’s previous ideas were?

<sup>526</sup> East, “Report of the Agronomist,” 426.

<sup>527</sup> Note that much of Castle’s argument is that selection does not reduce variability.

<sup>528</sup> East, “Report of the Agronomist,” 433. In this context, East was criticizing the “Lamarckian belief that continued improvement in tuber formation has led to degeneration of the sexual functions.” Instead, East argued that it was an inherited character, not a life history trade-off.

experiments with fluctuations, were obtained from homogeneous material. Johannsen's work has thrown into considerable doubt the homogeneity of natural populations. He has, moreover, concluded that the selection of fluctuations has nothing to do with the improvement of a race. Probably no other conclusion of recent times is so important to plant breeders. The work should certainly be duplicated along as many lines as possible; for its corroboration would not only sound the death knell of methods of improvements by the selection of partial fluctuations, but would entirely change our conception of procedure in other breeding operations. ... Furthermore, if Johannsen was correct, then *"no improvement can be made by selecting plus fluctuations in potatoes, except upon the intervention of mutative changes."*<sup>529</sup>

East found improving potatoes upon this conception exceedingly difficult, however, because "results have been obscured by seasonal, climatic and local soil conditions which have a tremendous effect and which are not constant enough to permit tracing marked hereditary transmission." Observed changes could be the result of mutation as well as fluctuations resulting from variation in health or age, among other factors. Putting to work a theory that rested upon detecting these minute differences could be rather troublesome, enough so that he ended the experiments following uncontrollable disasters (fire and drought).<sup>530</sup>

Shull continued to elaborate upon his "pure-line method in corn breeding." In an address to the American Breeders' Association, Shull claimed to have confirmed his previous conclusions that an "ordinary field of corn" is composed of complex hybrids. As East had pointed out, a major result of the pure line work was that it threw into "considerable doubt the homogeneity of natural populations."<sup>531</sup> Furthermore, they had reinterpreted the impact of inbreeding and self-fertilization: "the deterioration which takes place as a result ... is due to the gradual reduction of the strain to a homozygous condition." Both pedigree selection and mass selection reduced a population's variability, towards homozygosity, although at different rates, the latter more slowly due to the

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<sup>529</sup> East, *A Study of the Factors Influencing the Improvement of the Potato*, 401–3. East critiqued de Vries and Johannsen for their neglect of "bud mutation," which he thought of as no different than germinal mutations. However, East studied existing data regarding utility and concluded that most bud mutations were not progressive, but regressive (loss of character), and thus, likely useless except for flower colors. Edward M. East, "Suggestions Concerning Certain Bud Variations," *The Plant World* 11, no. 4 (1908): 83.

<sup>530</sup> Edward M. East, "Inheritance in Potatoes," *The American Naturalist* 44, no. 523 (1910): 424. This problem was also of concern to Jennings and MacDowell, discussed at length below.

<sup>531</sup> East, *A Study of the Factors Influencing the Improvement of the Potato*, 401–3.

problem presented by non-inheritable fluctuations as well as crossing.

Shull now had new ideas for how breeders should look to “find and maintain the best hybrid combination.” Crosses between “unselected” strains (i.e., inbred with no concern for yield or other traits) produced individuals with slightly higher yield than the continuously crossbred controls. Therefore, “... the result is sufficiently striking to suggest that the method of separating and recombining definite pure-lines may perhaps give results quite worth striving for.”<sup>532</sup> Because this method selected for the most heterozygous individuals, the high yield could not persist because heterozygosity segregates in the following generations. The upshot was that by maintaining homozygous self-bred stocks, the material from which to create vigorous hybrids remained the same through the generations (barring mutations), allowing breeders to repeatedly remake optimal crosses.<sup>533</sup>

Ironically, East and Shull had potentially arrived at a method to improve maize, not so much by directing the species’ evolution in a certain direction, but by freezing stocks to remake the same combination at will. To arrive at these techniques, East and Shull had adopted the stances, generally, of Hugo de Vries and Wilhelm Johannsen, both of whom were critical of Darwinism (as it was commonly interpreted). Their conclusions were contradictory to Castle’s in a straightforward way: Castle argued that selection *created* variation, whereas Shull and East argued that selection *eliminated* variation; although in artificial conditions, they thought selection could be used to maintain hybrid combinations. Because of these stark differences in theory as well as their implications for breeding techniques, the Mendelian-mutationism of Shull and East, conflicted with

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<sup>532</sup> George Harrison Shull, “A Pure-Line Method in Corn Breeding,” *Journal of Heredity* 5, no. 1 (1909): 52–56.

<sup>533</sup> Shull, 57–58. Shull explained this again in 1911 with regard to the success of the Illinois maize experiment. He wrote, their success can be “readily explained on the ground that some hybrid combinations of genotypes have greater capacity for the production of the desired qualities than other combinations, and that the selection has gradually brought about the segregation of those genotype-combinations which had the highest capacity for the production of the desired qualities. ... the results were dependent, not upon the isolation of pure types possessing the desired quality, but upon the securing and maintaining the proper combination of types. ... As a consequence of this [Mendelian segregation], no strain of corn can be maintained at a high value with respect to any quality whose development is correlated with heterozygosis, except by continued selection for the particular qualities desired. If in any such specialized strain selections should be made for a few years on the basis of some character independent of the one used in establishing the strain, the superior qualities for which it was originally selected would quickly disappear, owing to the breaking up of the efficient combinations which had been segregated and maintained by selection. George Harrison Shull, “The Genotypes of Maize,” *The American Naturalist* 45, no. 532 (1911): 249–50.

Castle's genetic Darwinism or selectionism.

The early history of hybrid maize demonstrates the interpenetration of theory and practice. Inbreeding had long been considered mostly deleterious, sometimes used to fix traits (as with Bakewell) but overall unhealthy for a population. This view was bolstered by Darwin's own experiments. Through their own experimental work, Shull and East did not necessarily overturn the view in general, but instead challenged the nature of the relationship between inbreeding and vigor – it was correlative, but not causative. This refinement allowed them to take greater control of maize: it had thus far escaped the fluctuation-mutation distinction of Mendelian-mutationism, but was now integrated into the evolutionary theory, a theory that itself was grounded in practical developments.

### **Herbert Spencer Jennings and Selection's Ability to See**

Herbert Spencer Jennings was also among the first Americans to corroborate the pure line theory. A biologist who had made his name studying the behavior of the “lower organisms,” Jennings expanded his studies of *Paramecia* to include variation, heredity, selection, and the inheritance of acquired characters.<sup>534</sup> Jennings' two publications on *Paramecia* were extensive — each over 100 pages long; his thoroughness and attention to detail would lead Castle, pure line theory's chief experimental critic, to consider them better evidence than Johannsen's own original publication. Although he developed his work independently of the other pure line workers, including Johannsen, Jennings developed rather similar theories regarding the interaction between selection, heredity, and variation. Like East, Shull, and Castle, Jennings' research is best understood as another instance of experimental evolution, rather than genetics, particularly because it was unclear at the time if the “lower organisms” had genetics. Unlike the others, however, he was not as interested in application and control, representing a more “pure science” approach. Rather than make analogies between nature and artifice, Jennings became primarily concerned with how his experimental results seemed to conflict with the “demands” of evolution in nature. Like Castle, Jennings' experimental methods

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<sup>534</sup> H. S. Jennings, “Heredity, Variation and Evolution in Protozoa. I. The Fate of New Structural Characters in Paramecium, in Connection with the Problem of the Inheritance of Acquired Characters in Unicellular Organisms,” *Journal of Experimental Zoology* 5, no. 4 (1908): 577–632; H. S. Jennings, “Heredity, Variation and Evolution in Protozoa. II. Heredity and Variation of Size and Form in Paramecium, with Studies of Growth, Environmental Action and Selection,” *Proceedings of the American Philosophical Society* 47, no. 190 (1908): 393–546.

eventually led him to reject pure line theory and Mendelian-mutationism, but his conversion to selectionism will be presented in the next chapter as the proponents of competing theories debated and conflicted.

Jennings chose his experimental organisms deliberately. Due to his career choice of organism — asexually reproducing microorganisms — Mendelism played little role in his work.<sup>535</sup> In fact, he considered the avoidance of such, which “tremendously complicates the study of heredity in higher animals,” a virtue of his research. An additional virtue of microorganisms was that they are “essentially free germ cells that are subjected to the immediate action of the environment, both direct and selective,” the distinction between the two actions being of prime importance.<sup>536</sup> Although they were difficult to measure,

unicellular animals present all the problems of heredity and variation in miniature. The struggle for existence in a fauna of untold thousands showing as much variety of form and function as any higher group, works itself out, with ultimate survival of the fittest, in a few days under our eyes, in a finger bowl. For studying heredity and variation we get a generation a day, and we may keep unlimited numbers of pedigreed stock in a watch glass that can be placed under the microscope.<sup>537</sup>

These are the same virtues that microbial experimental evolutionists point to today. But, before molecular biology and modern microbiology, studying these organisms did not appear to have immediate application. They *could* help make evolution visible: Jennings believed that “here if anywhere we should see readily the effects of environment and of selection in modifying a race.”<sup>538</sup> Even if academic, experimental evolution with a microbe was relevant in the surrounding debate centered mostly on maize and rats.

Jennings’ method was primarily biometrical, following Davenport. He collected *Paramecia* from a pond, measured their dimensions, reduced the data to statistical tables, and graphed the data. By studying wild-borne *Paramecia*, Jennings sought to dissolve the barrier between the natural and the artificial. His first sample contained four hundred

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<sup>535</sup> Although Mendelism does not appear in this work, Jennings soon contributed to the chromosome theory of heredity in collaboration with the Morgan laboratory and published on the mathematics of Mendelism.

<sup>536</sup> H. S. Jennings, “Heredity and Variation in the Simplest Organisms,” *The American Naturalist* 43, no. 510 (1909), p. 322.

<sup>537</sup> *Ibid.*, p. 321.

<sup>538</sup> *Ibid.*, p. 322.



individuals taken at random, killed with a chemical “known to cause practically no distortion when properly used.” To observe such minute organisms, taken by the drop and measured on the scale of microns, Jennings projected light through the slide onto paper, later measured by scale.<sup>539</sup> When Jennings cultured multiple populations at once, the need for meticulous measurement, combined with the organism’s rapid multiplication, caused Jennings to “probably” lose half of his experiments.<sup>540</sup> Thus were the difficulties of experimental evolution.

His results were remarkably like Johannsen’s, East’s, and Shull’s regarding pure lines, the inheritability of variation, and the power of selection, despite being conducted apparently without knowledge of the previous work. Jennings immediately distinguished two sets of *Paramecia* within his experimental population. Following months of isolation and propagation he concluded they were previously described (albeit contested) species: the smaller, *P. aurelia*, and the larger, *P. caudatum*. Jennings propagated a “pure line” of *Paramecia* under uniform conditions, measuring size, and found that “the progeny of large and of small individuals (within a given pure line) *showed no characteristic differences in size*.”<sup>541</sup> Jennings had independently corroborated the pure line theory.

Jennings went beyond Johannsen in important ways, however. He took extensive pains — roughly half of the 128-page article — to analyze the effects of growth and environment on individual size. Before considering these effects, attributing anything to internal factors would be unjustified. As would become a problem, continuous traits such as size were also traits of growth, muddying the results. (A strength of Castle’s work was that coat color was independent of growth.) But Jennings had little choice, given that *Paramecium* are “so minute and relatively differentiated an animal.”<sup>542</sup> As East had discovered with potatoes, external factors such as nutritional changes could nearly double the breadth of the organism within a week, problematic enough that Jennings excluded breadth as a reliable trait.

Jennings concluded that growth and environment caused the variation within a

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<sup>539</sup> Jennings’ precision was to the half micron; the first sample ranged in length from 84 to 164 microns.

<sup>540</sup> Jennings, “Heredity, Variation and Evolution in Protozoa. II. Heredity and Variation of Size and Form in *Paramecium*, with Studies of Growth, Environmental Action and Selection,” 500.

<sup>541</sup> Jennings, 405–6, 408.

<sup>542</sup> Jennings, 501. This is more a comment on the techniques available at the time than a factual property of the species.

pure line and were thus non-inheritable. (He did not use the term “fluctuation.”) His analysis had shown selection was of no effect in that it was “difficult or impossible to produce other races *within* these pure lines.” However, “there remains, of course, the possibility that still other lines exist in nature. Can we find in a ‘wild’ culture, by proper selection of differing individuals, still others of differing size?”<sup>543</sup> From a new wild culture, Jennings isolated several lines, but due to experimental contingencies, they lived under different conditions from his first cultures, and when brought together, some lines perished (i.e., selection). Thus, Jennings had to gradually acclimate each line to the same conditions, complicated by the fact that transferring an individual also entailed transferring some of the old medium, especially different strains of bacteria, necessitating a washing scheme. Once completed, Jennings propagated the cultures for about two weeks and determined that he had four distinct lines of *Paramecia*. In a new population cultured with the intention of testing the effects of growth, Jennings detected three new lines. Therefore, while size was a continuous trait, and thus the variability of lines overlapped, there were distinct and inheritable differences in size between the lines, just as Shull had discovered in a field of maize. (See Figure 5.)

Like Castle, Jennings was interested not only in the state of variation and heredity *within* these two groups, but wondered about selection’s power, asking “can we by selection and propagation produce within the limits of a single group races of different mean size?”<sup>544</sup> That is, could selection create a new pure line or in a way, ‘bridge the gap’?

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<sup>543</sup> Jennings, 485.

<sup>544</sup> Jennings, 407, 503.

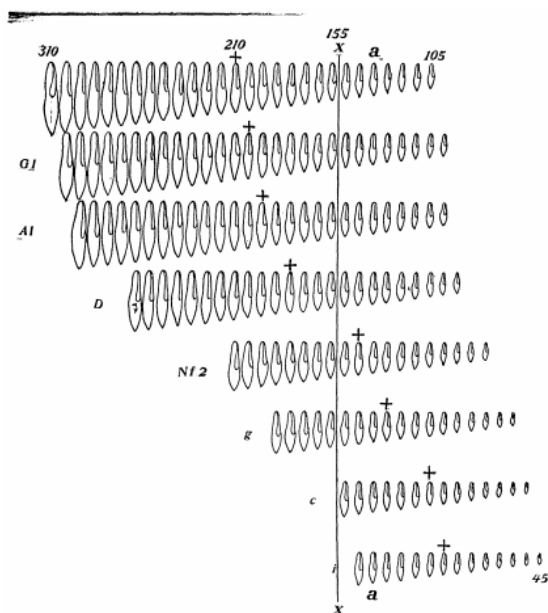


FIG. 5. Diagram of the species of *Paramecium*, as made up of the eight different races of Fig. 3. Each horizontal row represents a single race. The individual showing the mean size in each race is indicated by a cross placed above it. The mean of the entire lot is shown at *x-x*. The numbers show the measurements in microns. The magnification is about 43 diameters.

Figure 5: From Jennings, “Heredity and Variation in the Simplest Organisms” (1909), Fig. 3. Jennings pointed out that individuals of size “a” occur in all eight races, showing that appearance alone cannot identify an individual as belonging to a certain race; rather, “breeding is the only test” (pp. 329-330). This also shows why Jennings was concerned whether selection could identify these pure lines.

Jennings began a long-term selection experiment, their fast

reproductive growth and microscopic size allowing in months what Castle, East, or Shull would not be able to do in over ten years of work with animals and plants. Taking one of the original stocks — likely at 250 generations of culture in less than a year —, Jennings separated large from small and allowed the two cultures to multiply for seventeen days.<sup>545</sup> The mean dimensions were identical. Measurements over the next several weeks showed variation in mean size, but rather than further separating, the trend lines crossed, from which Jennings interpreted the variation as non-inheritable. In another experiment, Jennings selected a larger stock to become larger and a smaller stock to become smaller; fourteen generations later, these stocks also reversed. Jennings continued the experiment over the next month — five rounds of selection — and the stocks, despite directional selection, fluctuated randomly. Thus, “the results of selection, if there are any, quite disappear in comparison with the effects of slight environmental differences.” Jennings reported that “many other attempts were made to break a pure line by selection into

<sup>545</sup> Jennings had also changed the “basis” of selection to account for growth over time (age) by propagating both the largest and smallest individuals. “Therefore, the best method of procedure will be to take an old strain, which, derived from a single individual, has for a long time been multiplying freely without conjugation. From this the largest and the smallest individuals should be separated and allowed to propagate under identical conditions. If hereditary variations in size have occurred, we should in this way reach the same result as by actual selection and isolation through many generations. Physiological isolation has been as complete as would be experimental isolation.” Jennings, 506.

several lines; on this point an immense amount of work was directed.” Countering the commonplace that experimentalists did not allow enough time for evolution to occur, he wrote, “In the experiments described above, though their futility seemed evident from the first results, the work was continued for many generations, in order that failure might not be due to lack of perseverance.”<sup>546</sup>

Jennings was troubled by the nature of selection and mutation in evolution that emerged from his experiments. Selection’s power was again relegated to isolation — it was effective within a mixed population of pure lines, but once the population was reduced to a single line, its effects ceased (like when self-fertilized maize became homozygous). The ubiquitous variation in *Paramecium* was due solely to growth and environmental action, such as nutrition and “injurious bacteria.”<sup>547</sup> But because he had not detected a single inheritable variation, large or small, the origin of these pure lines remained unanswered; mutations were “much rarer than had been supposed.”<sup>548</sup> As evolution had come under exact experimental and statistical scrutiny, the theory apparently could not account for its reality: how could selection detect inheritable differences within a morass of non-inheritable variation? And how could selection-as-isolation result in the evolutionary progress from microorganisms to humans?

This was what I call “Jennings’ Problem.” His view of selection’s power was pessimistic, not only within an experimental setting, but in nature as well. Jennings echoed East’s methodological problem with external factors masking genetic differences in potatoes, expanding it to a theoretical conclusion about nature. He wrote,

We must consider, however, that if the non-inheritable differences are so much more numerous and marked than the inheritable ones as to render conscious selection by human beings ineffective, they would apparently have the same effect on selection by the agencies of nature. The same ground for selection offered by heritable variations is offered so much more fully by those not inheritable that there would be as little effect in selection by nature as in selection by man.<sup>549</sup>

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<sup>546</sup> Jennings, 506–509.

<sup>547</sup> Jennings, 518–22.

<sup>548</sup> Jennings, 524.

<sup>549</sup> Jennings, 522. Note that Jennings was already wondering whether “slight variations” and “mutations” were merely two ends of a spectrum, rather than physiologically distinct processes, something he reiterated in 1917. It would be interesting to compare this work with the later population genetics work on slight selective differences.

That is, in both potatoes and paramecia, selection acted upon the variation within a population, but if most variation was non-inheritable, selection would have trouble even performing its isolating effect. Jennings did not argue for selection's irrelevance; instead, he could not figure out how evolution could work.

Thus, like East and Shull, Jennings did not adopt the extreme view that selection was unimportant or ineffective. When he presented the "Evidence on the Effectiveness of Selection" to the American Society of Naturalists, he declared that "by methodical and progressive selection striking results can be reached." That is, it had the power to isolate. "From a wild culture ... By properly regulated selection a great variety of permanently differentiated lots are obtainable." However, when dealing with an individual line, selection produced "not the faintest trace of effect," even over hundreds of generations; "the race or line is absolutely permanent," "unyielding as iron." The differences that did exist were not inherited and therefore "they furnish absolutely no foothold for selection." Thus, "the effects of selection have then consisted simply and solely in isolating races that already existed."<sup>550</sup>

With Johannsen's introduction of the "genotype" in 1909, Jennings extended his conclusions to sexually reproducing species, or "biparental inheritance." Specifically, a genotype was a "set of individuals which, so long as they are interbred, produce progeny that are characteristically uniform in their hereditary features, not systematically splitting into diverse groups." Jennings illustrated how the "genotypic explanation of the effects of selection" could fit with biparental inheritance:

Organisms in which selection has shown itself effective are composed of many genotypes. ... From such a mixture of genotypes it is possible to isolate by selection any of the things that are present—perhaps in a great number of different combinations. ... But from such a mixture it is *not* possible to get by methodical selection anything not present. ... [or] anything lying outside the extremes of the genotypic characters already existing. ... In the case of genotypes that cross-breed readily, we may get an indefinite number of combinations of all that lies between the extremes of the existing genotypes—the variety of combinations realized depending on the rules of inheritance.<sup>551</sup>

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<sup>550</sup> H. S. Jennings, "Experimental Evidence on the Effectiveness of Selection," *The American Naturalist* 44, no. 519 (1910), pp. 136–137.

<sup>551</sup> Jennings, "Experimental Evidence on the Effectiveness of Selection," 139–40. Emphasis original. When

Jennings' 1910 articulation of evolution is remarkably prescient with respect to the theory of evolution that later emerged from population geneticists that emphasized recombination as a major source of variation. Jennings was not discussing actual recombination, the exchange of genetic material between chromosomes in sexual reproduction, but was pointing to the importance of genetic mixing within a population. This demonstrates that these biologists had a sophisticated understanding of genetics and selection, and that given their anti-Darwinian bent, that this emerging theory of evolution had a non-Darwinian character.

Using both his pure line work and Johannsen's notion of the genotype, Jennings contextualized, supported, and critiqued the work of others. As he had completed his work, he found that Johannsen, Pearl, Shull, and de Vries, among others, had reached the same conclusions about selection, isolation, and pure lines. Others, however, such as Galton, Fritz Müller, de Vries (in some of his experiments), and Castle "had reported definite progress as a result of methodical selection. Why this difference? Is there one law for the Jews, another for the Gentiles?" Jennings thought not, instead alleging that it was due to disparate attention to an experiment's initial conditions. Because Jennings, too, had found selection to be effective, but within mixtures and only until a single race was left, Castle's mistake was to have not accounted for this. Castle's stocks were of "complicated descent; they plunge us at once into all the difficulties due to interweaving, blending and transfer of characters from one genotype to another. ... MacCurdy and Castle got by selection all sorts of conditions lying between the extremes with which they started ... but they do not give us evidence that methodical selection can produce anything beyond combinations of what already exists."<sup>552</sup> That is, "bridging the gap" did

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compared to later evolutionary work, it is possible that what Jennings was missing was that rare combinations could potentially lie outside the extremes of what was then present. As is, Jennings' interpretation of genotype fit well with Shull's and East's ideas at this time.

<sup>552</sup> Jennings, "Experimental Evidence on the Effectiveness of Selection," 137–38, 140–41. Müller's and de Vries's experiments with maize did not account for male parentage and selection was actually "pick[ing] out the progeny of extreme male genotypes." De Vries' experiments on buttercups were troubling, but there were too many confounding variables to determine whether they fit or rejected a selectionist theory: the experiment did not begin with pure lines, "the variations dealt with are not out of the ordinary fluctuating sort (as de Vries points out); change in cultural conditions doubtless played also a large part." Jennings, 142. While Castle thought a replication of the buttercup experiment would shore up his position, Jennings thought it was not so certain. Citing the results of German breeders (Fruwith, von Rümker), Jennings argued, "continued methodical selection is often necessary, but what it does is to purify a contaminated

not account for the potential fact that both ends of the spectrum already exist within the genotype.<sup>553</sup>

To Jennings, the “pure line idea” was, like mutation, “an instrument for analysis of the entire field of variation, heredity, and evolution” — a “dissecting knife.”<sup>554</sup> Combined with Shull’s “peculiar tool” of the pedigree, the pure line work produced a critical methodological development: without pure lines, or without ensuring genetic purity within the stock, any work in experimental evolution was questionable. The initial conditions must be known “precisely.”<sup>555</sup> Hence Jennings’ choice of *Paramecium* was prescient: dealing with a non-Mendelian organism allowed him to separate signal from noise. He also had far less trouble moving back and forth between experiment and nature. Once he had contextualized his work within the broader field of experimental evolution, Jennings concluded that “the results of the analysis made by its aid indicate that most or all of the experiments in methodical selection have consisted in shifting about, isolating and recombining preexisting, permanent hereditary differentiations...”<sup>556</sup>

Jennings emphasized again that the pure line work did *not* entail that selection was unimportant; instead, it was limited by the nature of variation and heredity, i.e., Jennings’ Problem, partially resolved by mutation. “What the pure line work shows is that the changes on which selection may act are few and far between, instead of abundant; that they are found not oftener than in one individual in ten thousand...; that a large share of the differences between individuals are not of significance for selection or evolution... Thus the work of natural selection is made infinitely more difficult and slow; but logically it is still possible.”<sup>557</sup>

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race,” consistent with the pure line and genotype ideas (and as promulgated by Shull and East). Jennings, 141

<sup>553</sup> The irony of this conclusion is that Stoltzfus and Cable argue that what allowed Darwinism to revive under the Modern Synthesis was an emphasis on recombination as a source of small variation.

<sup>554</sup> Jennings, “Experimental Evidence on the Effectiveness of Selection,” 138, 141. He asked this as a rhetorical question; I changed it to a statement.

<sup>555</sup> Jennings, 136.

<sup>556</sup> Jennings, 143.

<sup>557</sup> Jennings, 144. In his conclusion, Jennings attacked the biometrical school, what was now a “small remnant (if there be such a remnant) of the biometrical school that still submits to the dictation of Pearson. ...How quickly the biometricians that devote themselves to careful biological investigations fall away from the Pearsonian faith. Darbishire, Davenport, Tower, Shull, Johannsen, Pearl; are there any biologists of achievement that still hold with Pearson? ... One of those sardonic paradoxes through which nature revenges herself, the men who from outside have lectured biology on the necessity of becoming exact are the strongest opponents of exact experimental and biological analysis. ... Those who find the

Jennings specified the need for pedigrees and careful measurement to make evolution visible, mostly through statistical analysis. After all, “the work with genotypes brings out as never before the minuteness of the hereditary differences that separate the various lines.” For example,

Johannsen found his genotypes of beans differing constantly merely by weights of two or three hundredths of a gram in the average weight of the seed. Genotypes of *Paramecium* I found to show constant hereditary differences of one two-hundredth of a millimeter in length. Hanel found the genotypes of *Hydra* to differ in the average number of tentacles merely by the fraction of a tentacle. That even smaller hereditary differences are not described is certainly due only to the impossibility of more accurate measurements; the observed differences go straight down to the limits set by the probable error of our measurements.

Jennings later emphasized that the smallness of hereditary differences supported a Darwinian theory, but here it was used in service of a theory that challenged the power and creativity of selection. Despite not having witnessed the origin of a new pure line, Jennings concluded from the pure line work in general that

Genotypes so differing have not risen from one another by large mutations. The genotypic work lends no support to the idea that evolution occurs by large steps, for it reveals a continuous series of the minutest differences between great numbers of existing races.<sup>558</sup>

Contrary to the general depiction of mutationists, Mendelians, or pure line theorists, one of their more generalizable conclusions was the minuteness of inherited variation. These differences were revealed by statistical analysis of large populations, and over time, selection, whether natural or artificial, was able to slowly isolate them. Jennings was open to the possibility that selection could be shown to be effective within a pure line or genotype, to “break” it, but setting a new standard, “the demonstrators will need to show precisely the relation of their results to the pure line concept.”<sup>559</sup>

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genotype idea useful may then prepare themselves for one of those justly famous bludgeonings from the dictator of the whilom orthodox biometrical school; this is the last honorable mark of distinction which stamps the investigator as a thorough and exact analyst of things biological.” Jennings, 143. See Kim, 1994 for more.

<sup>558</sup> Jennings, “Experimental Evidence on the Effectiveness of Selection,” 144–45.

<sup>559</sup> Jennings, 145.



Once again, it was not that Jennings desired to find selection ineffective; indeed, the results were puzzling (Jennings' Problem). His conclusion that selection "had produced nothing new" meant that his long-term experiment had also shown "no progress that would form a step, however slight, in the journey from *Amoeba* to man." Yet this contradicted what was "demanded" of natural selection: what evolution required was precisely the power to "produce progress from *Amoeba* up to man." Evolution must somehow "produce, from a given condition, something that did not before exist in that given condition."<sup>560</sup> Beyond mutations which he himself had not witnessed in his work, Jennings had no answer. When combined with Shull's practical work focusing on processes unlikely to occur in nature (frozen inbred lines hybridized continually), the experimental study of evolution had rendered it apparently historical improbable. The major exception was Castle's systems of hooded rats and polydactylous guinea pigs, but a contingent of his colleagues now thought there were serious methodological problems with his work.

The following year, Jennings spoke again before the American Society of Naturalists on pure lines and genotypes in *Paramecia*, in which he asserted their "actual existence" as "concrete realities" due to "facts that strike you in the face."<sup>561</sup> He had even witnessed selection occur between them. He considered pure lines to be "*different method[s] of responding to the environment*," particularly in their rates of multiplication and conjugation (and had been able to distinguish this from their dependency on environmental conditions). These differences produced

striking cases of natural selection between genotypes. ... If we place together in the same culture two genotypes of *Paramecium*, as I have many times done, almost invariably one flourishes while the other dies out. This ruins many a carefully planned experiment; it must take place on a tremendous scale in nature.<sup>562</sup>

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<sup>560</sup> Jennings, 136–7. This was not an entirely new worry or critique of Darwinian evolution. It is to some degree a rehashing of the canard that goes "what use is half an eye?" that Darwin countered in the *Origin*. But importantly Jennings was now discussing small changes such as mutations in body size in *Paramecium*. Furthermore, Jennings was not discussing so much adaptive value, but whether a given hereditary change was large enough to not be masked by fluctuations. This worry was perhaps resolved by theoretical population genetics, such as Norton's table in Punnett's *Mimicry in Butterflies*, discussed by Stoltzfus and Cable, "Mendelian-Mutationism: The Forgotten Synthesis," 525 and Provine, *The Origins of Theoretical Population Genetics*, 137–139.

<sup>561</sup> Jennings, "Pure Lines in the Study of Genetics in Lower Organisms," *The American Naturalist* 45 (1911): 79–89.

<sup>562</sup> Jennings, 84.

Thus, Jennings saw an additional virtue of his experimental organism as not needing to account for the artifice of laboratory experimentation, instead it was “ruining” his work. He did not witness artificial selection, but “natural selection between genotypes.”

Therefore, Jennings could now report “with pleasure” that “wild populations ... include many genotypes” and the

extensive operation of selection among the diverse existing lines, and particularly in this extensive production of new combinations at conjugation, with cancellation of many of the combinations. ... Numbers of the strains produced die, or multiply so slowly that they have no chance in competition with those that are strong and multiply rapidly. Thus many of the combinations produced are canceled; only the strongest combinations survive. We have then on a most extensive scale an operation in natural selection and the survival of the fittest; the production of many combinations, some of which survive, while others fail.<sup>563</sup>

Perhaps evolution was now the survival of the best genetic combinations. All that was needed for “evolutionary progress,” still, was to discover how “diverse genotypes must have arisen from one...”<sup>564</sup> He thus lamented that while he had witnessed selection between types and combinations, he had not witnessed creative evolution:

When operating on a single isolated type it appeared that the progressive action of selection had not been seen. ... I hoped to accomplish this myself, but after strenuous, long-continued, and hopeful efforts, I have not yet succeeded in seeing selection effective in producing a new genotype. This failure to discover selection resulting in progress came to me as a painful surprise, for like Pearson I find it impossible to construct for myself a “philosophical scheme of evolution” without the results of selection and I would like to see what I believe must occur.<sup>565</sup>

But, hopefully, the pure line work had cleared the theory of evolution of its confusion and had set the stage for detecting evolution in action (despite introducing some new problems):

These are facts of capital importance to the experimenter; besides their theoretical significance, they open to each of us the opportunity to direct our efforts upon precisely

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<sup>563</sup> Jennings, 87–88, 90.

<sup>564</sup> Jennings, 90.

<sup>565</sup> Jennings, 88. Emphasis original.

this point, and so perhaps to be the first to see examples of this fundamental process not yet seen.<sup>566</sup>

In the end, Jennings “hoped” that “someone on our program, more fortunate than myself, will be able to record seeing the actual production of two genotypes from one, or the transformation of one into another, by selection, or in any way whatever.”<sup>567</sup> Ironically, it would be Jennings himself, concluding a new experiment in 1916, that would overturn both his belief in the pure line theory and his doubts concerning the frequency of inheritable variations and selection’s ability to act upon them.

### Conclusion

This chapter shows that the experimental evolution that studied the intersection of pure line theory, mutation theory, Darwinism, and Mendelism was both lively and fruitful. In contrast to Robert Kohler’s pessimism regarding the results of early experimental evolution, his thesis applies only to experimental evolution in the field. Experimental evolution in the laboratory, at least this subset of it, generated results and fueled debate on pure lines, gametic purity/contamination, and especially selection, even if the theoretical understanding remained somewhat inconclusive. However, fundamental questions and preliminary answers had been outlined, resting on distinct theories of variation, heredity, and selection. Selection – the more controllable evolutionary process – was either creative and the key to the human control of evolution as a whole (Castle) *or* it was merely an isolating and eliminative dynamic that depended upon extant variation (pure lines) and mutations, in which extreme inbreeding was an even more effective tool at human disposal even if not operative in nature (Castle’s opponents). (This led in turn to the question of controlling mutation, emphasized by MacDougall, Davenport, Blakeslee, and later, Muller, as discussed by Kingsland, Campos, and Curry.) That is, in East’s words, whether selection “altered the type” or “reduced variability.” Although the next chapter will show that most geneticists considered Castle’s theories and experimental systems to be fatally flawed, his opposition played an essential role in driving the theoretical and practical elements of the science forward.

By applying statistics, rearing organisms in controlled conditions, making

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<sup>566</sup> Jennings, 88–89.

<sup>567</sup> Jennings, 89.

pedigrees, and subjecting populations to selection and inbreeding, these experimentalists had made moves to bring evolution under control, at least within their laboratories and fields. They could now quantify the (in)effectiveness of selection and ranges of variation, observe the arrival of a mutation (or not at all), and determine the degree to which a trait was inherited. They had combined Darwin's experimental spirit with Mendel's exactness, with the push to control descended from the breeders and encouraged by the institutional and social context of capitalism.

Early geneticists are frequently referred to as "typological" thinkers, particularly in the view of evolutionary biologist turned historian/philosopher Ernst Mayr. While there is some truth to this claim, they were, I argue, in a *transition* between typological and populational thinking. Johannsen, East, Shull, and Jennings all emphasized that populations were made of types, hidden until revealed by experimental control. But they did not think of populations as an intermixed and recombining gene pools, at least not yet. That is, they apparently considered a biotype, or pure line, to be the basic ontological unit within their work, these lines then hybridizing with each other. Then again, the work on recombination, crossing over, and chromosomal mechanics in general, had not yet begun. They worked up from the pure line, rather than down from the population, based on the experimental evidence before them. Populational thinking arguably then rests on the developments that came out of the Morgan laboratory, and hence to denounce these experimental evolutionists as typological thinkers is anachronistic. To do so assumes that Darwin was right all along, and ignores that, as Stoltzfus and I argue, the Darwinism of the Modern Synthesis is *not* the Darwinism of Darwin. Rather, these experimental evolutionists took Darwin's theory, tested it experimentally in light of the work of de Vries, Johannsen, and Mendel, and found it wanting. They then ironically produced a body of work that provided the foundation for a "restoration" of Darwinism during the Modern Synthesis, which will be developed further in the next chapter.

One question their work raises though is whether the work was *too* artificial.<sup>568</sup>

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<sup>568</sup> S. Andrew Inkpen has examined this debate over the division between the artificial and natural with respect to Darwin, Dobzhansky, and Jared Diamond in "Denaturing Nature: Philosophical and Historical Reflections on the Artificial-Natural Distinction in the Life Sciences," PhD diss., (University of British Columbia, 2014) and "'The Art Itself Is Nature': Darwin, Domestic Varieties and the Scientific Revolution," *Endeavour* 38, no. 3–4 (2014): 246–56.

Jennings, not interested in breeding, avoided this issue, but East, Shull, and Castle arguably used methods that would not occur in nature: intensive inbreeding. (Think of how one of the conditions considered in Hardy-Weinberg equilibrium is the spectrum of random to assortative mating, of which inbreeding is an extreme form of the latter.) This is to some degree reflected in their comments on nature: Castle, as I will discuss, began his career in experimental evolution commenting frequently upon the implications for natural evolution, but once he took up a genetic Darwinism, stopped doing so altogether. Similarly, East and Shull questioned the validity of extrapolating their work into nature. East acknowledged that most experimentation still consisted of relatively few generations, but that worrying about the problem was impractical. Shull remarked that the extreme isolation he practiced likely did not occur in nature, but it also allowed for “perfect knowledge” of ancestry. One answer is that they simply did not care, and that the possibility to control evolution for practical purposes seemed so within grasp that for the moment, nature ceased to matter. This was amplified by many of these organisms being commodities whose yield (in capitalist society) became paramount, yield and profit acting as the proxies of the emerging notion of fitness. However, the Darwinian dialectic of artificial evolution being a form of evolution meant that it held theoretically productive power when carefully integrated with other scientific threads.

Through this chapter, Castle, East, Shull, and Jennings developed their systems and theories in relative isolation. In the next chapter, debates over the validity of pure lines, the effectiveness of selection, the importance of mutations, and other evolutionary questions erupted. This debate will also draw in figures not yet discussed — Raymond Pearl, the Morgan lab, especially Sturtevant, Bridges, and H. J. Muller, as well as the European breeder-scientists, the Hagedoorns. It was in this period, 1911-1919, that selection and genetics was reworked into a theory resembling Darwin’s and met the “demands” of evolution.

## **Chapter 5:** **“At Nature’s Mercy”: The Debate Over How to Control Evolution**

### **Introduction**

Despite more than a decade of debate, exactly how to control genetic evolution remained hotly contested. Up to this point, Castle had promulgated his new theories of variation, heredity, and selection relatively free of criticism. Once he definitively published his heresies, combined with his rejection of pure line theory and the multiple factor hypothesis, Castle’s work was subjected to a steady stream of attacks by other scientists engaged in experimental evolution: Raymond Pearl, Hermann J. Muller, Alfred Sturtevant, Calvin Bridges, the Hagedoorns, and even his former student, E. C. MacDowell. Only Jennings became sympathetic, but it took his own experimental work to be convinced, and even then, he took a middle road. These criticisms ranged across methods, data, interpretations, and even presentation, but Castle’s views only hardened until his sudden concession in 1919.

Through the 1910s, the subject of this chapter, experimental evolution began to merge with genetics. With East’s introduction of multiple factor theory, in addition to the Morgan laboratory’s interventions, Castle’s opponents integrated their theory of evolution with Mendelism and chromosomal mechanics. In contrast, Castle and Jennings downplayed the importance of chromosomal mechanics, relying more on the surficial or phenotypic effects of selection, a move their opponents rejected as violating core Mendelian principles. Yet Castle’s intransigence and Jennings’ conversion made selection’s creative power a notion their opponents had to contend with. Although they never used the term, they were forging a “synthesis” between Mendelism and natural selection. Castle may have played the role of the Darwinian, but it is the Mendelians who appear to be more “modern.” They denied the creativity of natural selection, but they still investigated its dynamic effects within genetic populations.

This chapter follows the debate over selectionism, mutationism, and Mendelism from 1910 to 1920, its implications for controlling evolution, and its contributions to evolutionary science in general. It begins with East’s and Shull’s Mendelizing of

selection through the former's articulation of the multiple factor theory, a way to explain continuous variation and blending inheritance through what is now called polygeny. Then I turn to Castle's theory of creative selection as an explanation of his hooded rats experiment using John Beatty's phrase of the "sliding scale."<sup>569</sup> I then address the debates that ensued between Castle and Muller, the Hagedoorns, and Raymond Pearl that bore on methods, results, and theory that interwove science and breeding. The next section covers Jennings' work with *Diffflugia* that convinced him to abandon the hardened pure line position for a more selectionist one. Following these debates, Castle, Jennings, and Pearl published in 1917 three papers that addressed the "selection problem" from a general vantage point. Here I use a set of correspondence between Jennings and Pearl to interrogate the subtleties of the "selection problem," showing further that there was much more at play than merely Mendelians rejecting the effectiveness of selection. Lastly, the chapter discusses the Drosophilist intervention in which they demonstrated the existence of modifiers which in turn explained phenotypic responses to selection. This work, combined with an experiment with the hooded rats suggested to Castle by Sewall Wright, convinced Castle to concede the debate in 1919 with the implication that evolutionary control remained out of reach.

### **East's and Shull's Mendelizing of Selection**

As Jennings, East, Shull, and others corroborated the pure line theory, they continued to develop and integrate it with Mendelism and breeding practices, shown by East's 1910 landmark publication, "A Mendelian Interpretation of Variation That Is Apparently Continuous." Usually depicted as a synthesis of Mendelism (discontinuous variation) and Darwinism (continuous variation), East did not interpret his own work in this way, as he revealed with an additional paper that year, "The Role of Selection in Plant Breeding." Given the tendency to misconstrue some of the specifics of the period's theoretical and experimental disputes, I will also show how East can easily be misread as a Darwinian. For both Shull and East, this period was one of further consolidation around the work of de Vries, Johannsen, and Mendel, as they extended their experimental work

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<sup>569</sup> John Beatty, "The Creativity of Natural Selection? Part I: Darwin, Darwinism, and the Mutationists," *Journal of the History of Biology* 49 (2016): 659-684.

to explain more of evolution, synthesizing genetics and selection.<sup>570</sup>

East claimed that biology was recapitulating the history of chemistry, transforming from an analytic science into a synthetic science. Shull also elaborated on biology's growing analytic power, writing that Darwin had "overthrow[n] the conception of permanency of specific types," convincing scientists that "everything is in a state of flux." However, Darwin's "appeals" to the experiences of breeders meant many of his ideas "were the result of no such careful control of conditions or analysis of results as has been found necessary for the discovery of genetic laws." Analytical tools, such as pedigrees and pure lines, and conceptual distinctions, such as mutation/fluctuation and genotype/phenotype, moved the science forward, but further entrenched within evolutionary theory a tension between permanence and fluidity.<sup>571</sup> This tension was the contradiction over which Jennings lamented and Castle rejected in favor of total fluidity.<sup>572</sup>

Now was the time of "heredity as an exact science," according to Shull, the "era of *experimental* evolution." The initial steps — Jordan's study of *Draba verna*, N. H. Nilsson's breeding work, and de Vries' synthesis of scientific and horticultural results — had culminated in the work of Johannsen.<sup>573</sup> Johannsen had also combined the positive aspects of Weldonian biometry (important methods with improper biology) with Batesonian genetics (which unduly emphasized "alternative types").<sup>574</sup> East also pointed to Johannsen's work, a "puzzle" that fit together pieces from de Vries, Galton, Pearson, Darwin, Weismann, de Vilmorin, and Le Couteur, "an explanation that should have been thought of before, but like many other important discoveries, it was too simple for ordinary minds to grasp."<sup>575</sup>

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<sup>570</sup> Edward East, "A Mendelian Interpretation of Variation That Is Apparently Continuous," *The American Naturalist* 44 (1910): 65–82; East, "The Role of Selection in Plant Breeding," *Popular Science Monthly* 77 (1910).

<sup>571</sup> These conceptual distinctions provided the "order" that allowed for scientists to exert power and control evolution. George Shull, "The Genotypes of Maize," *The American Naturalist* 45 (1911): 234. 236. This critique conforms to de Chadarevian's arguments about Darwin and the professionalization of biology.

<sup>572</sup> Shull's and East's comments about flux and permanency are examples of "unconscious" dialectics.

<sup>573</sup> I mentioned Jordan's study of *Draba verna* in Chapter 2; de Vries emphasized that Jordan had demarcated 200 "elementary species" within this Linnean species.

<sup>574</sup> George Shull, "Heredity as an Exact Science," *Botanical Gazette*, 1910, 226. Shull emphasized that differences between biotypes could be incredibly minute. See also Shull, "The Genotypes of Maize," 236–37.

<sup>575</sup> East, "The Role of Selection in Plant Breeding," *Popular Science Monthly* 77 (1910). Louis de Vilmorin



East and Shull praised how Johannsen's work had practical implications for both evolution and plant breeding. East pointed to Johannsen's populational perspective that emphasized a given crop as a mixture of genetic lines with heritable differences, as opposed to the ancestral lineage perspective of Galton and Pearson. Rather than explaining regression as the "pull toward mediocrity exerted by former ancestors," Johannsen characterized regression as a result of not controlling for crosses between superior and mediocre individuals.<sup>576</sup> Shull held the most important of Johannsen's contributions to be demonstrating "*the permanence of the elementary types*," an extension of de Vries' work, and now conceptualized within the distinction of genotypes and phenotypes first articulated in 1911.<sup>577</sup> He acknowledged that Johannsen, because of his new distinction, "dismisses all [evolutionary factors] which are not based upon" it, such as direct effects, Lamarckism, and even Weismannism. (Note, though, that these theories were falling away in general due to experimentation, including at the Station.) Thus, isolating a pure line, unaffected by permanent changes via environmental action or selection, from an initial mixed population, prevented regression and set the stage for the breeders' control of evolution.

For Shull and East, Johannsen's theory facilitated the further control of evolution; the past had less influence over the present. However, Shull was disappointed that

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was an important French commercial plant breeder, whose wheat the Hagedoorns used in their argument against Castle (discussed below). John Le Couteur was a nineteenth-century British Army officer who took up an interest in breeding, but unfortunately East did not explain his influence upon the art and science of breeding.

<sup>576</sup> Johannsen interpreted the same phenomenon to be "mixture[s] consist[ing] of sub-races each with a heritable difference in the character size." Thus, under the "German method of mass selection with poor control against mediocre pollen, the chances were overwhelmingly in favor of the selected type recrossing with the more commonly cultivated and poorer type from which it came." East and Hayes integrated this view with Mendelism: If one crossed two strains of maize differing in height, a product of "many contributing factors," the F<sub>2</sub> generation showed greater variability following a normal curve due to a combination of fluctuations and recombination. "This condition of affairs tends toward the maintenance of a general mean in height, but this mean is false. It is false because the modal class which Galton and Quetelet took to be the type toward which the species is tending actually contains more heterozygous individuals and individuals heterozygous for more factors than any other. An individual selected from this class is less likely to breed true than one selected from the extremes. Cross-fertilization, therefore, may tend toward the production of a mean that gives falsely an appearance of fixity of type." East and Hayes, *Heterozygosis in Evolution and in Plant Breeding*, vol. 243 (Washington, D. C.: Bureau of Plant Industry, 1912), 45.

<sup>577</sup> In Shull's words, genotypes were "collections of individuals having like germinal characters to distinguish them from mixtures of individuals having like external characters, but of unlike germinal composition [phenotype]." Shull, "Heredity as an Exact Science," 227–28.

Johannsen “devote[d] relatively little attention” to the *origin* of biotypes.<sup>578</sup> Shull suggested that new biotypes may arise from “changes in the characters of the genes or determiners, loss of genes, combinations of different genes through hybridization, etc.” But like Darwin, he was frustrated by the lack of causal knowledge, a lack which in turn curtailed controlling evolution.

East himself provided a theoretical boon to Mendelism in 1910 through “multiple factor theory.”<sup>579</sup> East forwarded and corroborated the work of Swedish botanist and geneticist Herman Nilsson-Ehle, in which “the curve of variation simulates the fluctuation curve, with the difference that the gradations are heritable.”<sup>580</sup> In essence, East and Nilsson-Ehle independently showed that a continuous trait (such as size or color) could be considered “the concrete result of the inter-action of several cumulative units affecting the same character” (what is now called polygenism). The key was to raise enough offspring: if a trait were made of four units, only one of every 256 individuals would be purely recessive, “a larger number than is usually reported in genetic publications.” East demonstrated maize’s consistency with this principle through dihybrid combinations of dominant yellow and recessive white: if too few individuals were grown, the probable result was a mix of yellows, e.g., non-Mendelian, *but* in larger samples, whites appear in a ratio of 1 to every 15. The more factors and the more incomplete the dominance, the more mixed the blend, the more the trait approached continual gradation — a possible explanation of Castle’s hooded rats. The theory had explanatory power.<sup>581</sup>

Usually presented as a synthesis of Mendelism with Darwinism or biometry, East’s comments indicate that it was simply an extension of Mendelism into cases normally considered outside its bounds. Expanding upon Johannsen’s reinterpretation of the genetics of populations, the new hypothesis eliminated the biometric modal “type,” “around which variants converge”; instead, the mode was likely heterozygous for several

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<sup>578</sup> Shull, 228.

<sup>579</sup> Note that this theory was not wholly new: Bateson and Saunders, for example, had proposed this scheme in their first genetics publication. See Stoltzfus and Cable, “Mendelian-Mutationism: The Forgotten Evolutionary Synthesis.” Castle ironically had also picked this up, albeit briefly.

<sup>580</sup> East, “A Mendelian Interpretation of Variation That Is Apparently Continuous,” 73. East reiterated that “fluctuation” referred to “somatic changes due to immediate environment, and which *are not inherited*.”

<sup>581</sup> East, 72, 75, 81. Emphasis original. East noted one possible exception, but “this is only an hypothesis, and while I have faith in its foundation facts, the details may need to change.” East, 81. Soon East expressed more confidence, in East, “The Role of Hybridization in Plant Breeding,” *Popular Science Monthly* 77 (1910), and East and Hayes, *Heterozygosis in Evolution and in Plant Breeding*: 34–35.

units that would break apart due to segregation.<sup>582</sup> The reliance on biotypes in Shull's "Composition of a Field of Maize" had given way to a view more akin to gene pools.

East immediately realized the negative implications this theory had for Castle's work: that characters could be the result of multiple factors entailed that "the term unit-character [had] less of an irrevocably-fixed-entity conception." Castle's single quantitatively-varying factor might instead be several independent units, mostly undetectable with small population sizes. East asked, "can it be said that anything has heretofore been known concerning the actual gametic status of [the] parents...?"<sup>583</sup> The multiple factor theory further cemented the methodological need to know the initial conditions of a population's genetics.

In a prescient passage, East thought that the multiple factor theory even gave "a rational basis for the origin of *new* characters, which has hitherto been somewhat of a Mendelian stumbling-block." For example, East considered "biological isomerism," in which multiple "Mendelian unit forms" contributed to the same character but were not allelomorphs, perhaps differentiating in the past and now becoming dihybrid when hybridized. Or, "several of these quantitative units which produce the same character may become attached like a chemical radical and again behave as a single pair." In any case, East concluded that the hypothesis would "add another link to the increasing chain of evidence that the word mutation may properly be applied to any inherited variation, however small..."<sup>584</sup>

East again reevaluated the Illinois corn experiment, now in light of the multiple factor theory, illustrating the subtle theoretical differences that had emerged among experimental evolutionists. The experiment had begun in 1896 "with a hazy Darwinian idea that as corn was known to vary in composition, continuous selection of extreme variations would produce a continuous change in type." Success in increasing or reducing oil and protein content "clearly show[ed] the rapidity with which results can be obtained by this method of selection..." Indeed, "selection ha[d] been the main cause of improvement" of the United States' "agricultural wealth." From this, one may conclude

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<sup>582</sup> East, "A Mendelian Interpretation of Variation That Is Apparently Continuous," 80.

<sup>583</sup> East, 81-82.

<sup>584</sup> East, "A Mendelian Interpretation of Variation That Is Apparently Continuous," 82.

that East was Darwinian. *However*, by “selection,” East meant “the isolation of superior strains” via “detection [and] a sufficient increase for commercial use.” East’s counter-interpretation of the Illinois corn experiment was now as follows.

The published records showed that the variability of the strain was but little, if any, reduced by continuous selection. With extreme variants comparatively as far removed from each year's type, available for planting in each successive generation, the gain each year should have been at the same rate, *if the Darwinian interpretation of the role of selection were correct. On the contrary*, we notice that the regular curve fitted to the crop averages for ten generations, is first concave showing great progress made by selection, is later convex as progress becomes slower, and last becomes horizontal as no more progress results. It is very evident that the original stock was a mixed race containing sub-races of various composition intermingled by hybridization. Selection rapidly isolated these sub-races. The isolation was practically complete at the eighth generation in the case of the protein strains and the ninth generation in the oil strains. After this selection accomplished nothing. That the effect of selection was simply the isolation of a sub-race and not a continuous response, is further demonstrated by the fact that in 1903 another plot was started with seed from the isolated high oil strain. After four years' cessation of selection, the average composition of the crop remained the same, showing that after complete isolation of a homogeneous type no retrogression of the selected character occurs unless intercrossing with mediocre strains takes place. Fluctuation in composition still appears, but this is the non-inherited kind produced by external conditions.<sup>585</sup>

Selection’s effect was to isolate, not create. Selecting fluctuations led to no permanent change; instead, mutations served as “the basis of selection. They are constant from the beginning and remain so unless changed by a second variation...” Still of unknown frequency, he suggested that mutation size is “controlled” by the “mathematical law of error,” in that small mutations were likely far more frequent than large ones.<sup>586</sup> What this meant for the agent of selection was that they had to wait for mutation. He wrote,

the whole aim and action of selection is to detect the desired heritable variants among the useful commercial plants and through them to isolate a race with the desired characters.

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<sup>585</sup> East, “The Role of Selection in Plant Breeding.”

<sup>586</sup> East continued to adopt de Vries’ distinction between progressive and retrogressive variation, but now considered degressive to be unnecessary, now explained as latency. He suggested that “the relative value of progressive and retrogressive variations is difficult to estimate. In *organic evolution* the former must have been far more valuable; *commercially* the latter are often of great worth.” Ibid.

When this is accomplished, *selection can then do nothing until nature steps in and produces another desirable variation*. In other words, the results of selection are not continuous. Selection does not gradually perfect a character. The production of heritable variations is intermittent and the intermissions may be long.<sup>587</sup>

But he also remarked on how selection could *appear* to make continuous progress:

If the practical results seem to be parts of a continuous process, it is because of the imperfect methods at hand to isolate the desirable variations from their combinations with undesirable characters formed by natural hybridization [heterozygosity].<sup>588</sup>

This view of mutation and selection was an early articulation of a “lucky mutant” point of view and also accounted for genetic heterozygosity as a complicating factor. Shull also reinterpreted the work in Illinois on maize in non-Darwinian terms. Begun long before the articulation of Shull’s and East’s new explanations, the Illinois work could not have consciously accounted for them in their experimental designs:

[That] the fact that yield and perhaps many other qualities attain their highest development in the case of complex hybrids naturally leads to the *unconscious selection of heterozygous plants* for the next year’s cultures, and the continual breaking up of these complex hybrids in subsequent generations gives a result which closely resembles fluctuating variation, but which is fundamentally different from it. The genuineness of the gains made by selection in corn might naturally lead to the conclusion that fluctuations are inherited were it not for the abundant evidence now available showing that a considerable portion of the variation presented is not fluctuational, but is due to the presence of a mixture of different types which any selection partially segregates.<sup>589</sup>

Thus, Shull had worked out how the accumulative selection of fluctuations was illusory and could provide a coherent account of how it worked genetically through hybridization and heterozygous combinations. Summarizing his own work on the benefits of inbreeding in maize improvement, Shull referred to the self-fertilized stocks as “genotypically distinct,” selection showing them to have “different centers” around which they varied

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<sup>587</sup> Ibid. Emphasis mine.

<sup>588</sup> Ibid.

<sup>589</sup> Shull, “The Genotypes of Maize,” 252.

(such as in number of rows). As the breeder selected or isolated, strains “approach[ed] purity as a limit,” explained as the “distinct genotypes of maize ... gradually segregat[ing] from their hybrid combinations.”<sup>590</sup> Thus, East and Shull did not so much as reject the *appearance* of how selection, heredity, and variation interacted, but redeveloped their underlying mechanics.

Given that early Mendelians are frequently labeled as “typological” thinkers, it is unfortunate that Shull and East were ambiguous about the ontology of hybrids and pure lines. Did genotypes pre-exist in their hybrid combination or was it merely their origin? For example, Shull envisioned a “similar demonstration that populations of cross-breeding plants and animals are composed of fundamentally distinct types, intermingled but not changed by panmixia, and capable of being separated by appropriate means and of being shown to possess the discreteness, uniformity and permanence already demonstrated for the genotypes of self-fertilized and clonal races...” Under two interpretations, Shull meant that hybrids themselves were composed of “fundamentally distinct” pure lines *or* that a field of maize was a mosaic of pure lines. In the same paper, however, Shull writes that “self-fertilized families” are “derived originally from a common stock.”<sup>591</sup> The question at hand is: Were stable genotypes present within fields of maize or were genotypes artificial creations of the breeder? Whichever is the case, and taking note these publications predate robust theories of recombination, East and Shull show that geneticists were not uniformly “typological” thinkers, but could not yet grasp the “populational” outlook in its entirety, hence I argue that East and Shull took part in the *transition* from one to the other.<sup>592</sup>

Shull and East now labeled the phenomenon they had studied for several years as “heterozygosis,” fully integrating Mendelism with the pure line theory and the notion of “hybrid vigor.” According to Shull, “the degree of vigor is correlated with the degree of

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<sup>590</sup> Shull, 239–41, 246. Shull presented the evidence that vigor and inbreeding are separable phenomena: Breeding together two individuals within the same self-bred stock caused no change (because no new hereditary elements were introduced). The F<sub>1</sub> of a cross between two self-fertilized lines produced the most vigor because of high heterozygosity. “Crosses between sibs among the first-generation hybrids between two genotypes will yield progenies having the same characteristics, the same vigor, and the same degree of heterogeneity” as self-fertilizations of those sibs (i.e., a repetition of the first point).

<sup>591</sup> Shull, 246, 238, 240.

<sup>592</sup> See footnote 94 in Chapter 4 for evidence that Shull thought of biotypes and pure lines as originating by mutation but remaining distinct even within Mendelian hybrids, re-emerging in full in the F<sub>2</sub> generation.

heterozygosis.”<sup>593</sup> Maize was a “collection of complex hybrids,” heterozygous for many characters. The “sole function of selection” was to separate homozygous strains from each other.<sup>594</sup> In addition, “the effects of inbreeding are not to accumulate ill effects, but to isolate homozygous strains,” both “good” and “poor.” In practice, “complete homozygosis is approached as a variable approaching a limit” and was “difficult to obtain.” It also meant that selection and inbreeding were two forms of the same process of reducing heterozygosity: “From this illustration we think it is a fairly easy to see that no matter in how many characters a plant is heterozygous, continued inbreeding will sooner or later eliminate them. Close selection, of course, tends toward the same end, but not with the rapidity or certainty of self-fertilization.”<sup>595</sup> When homozygous strains were crossed, the next generation showed hybrid vigor or a “developmental stimulus” (heterozygosis). Decreasing vigor from the inbreeding of crossed species and increasing vigor from the crossing of self-fertilized species “are manifestations of one phenomenon. This phenomenon is heterozygosis.”<sup>596</sup>

The scientific upshot of the maize work on pure lines, genotypes, and heterozygosis, according to Shull, was that a “cross-bred plant like Indian corn harmonizes in its fundamental nature with such normally self-fertilized material as beans, wheat and other grains, and such clonal varieties as potatoes, paramecium, etc.” That is, the gametes “of even the most complex hybrids present a limited number of different types which can be assorted into homozygous combinations, and that, therefore, the progressive change resulting from continued selection may be simply explained as the gradual segregation of homozygous types or of the most efficient heterozygous combinations.”<sup>597</sup> This was Shull’s “peculiar tool” of pedigree keeping providing “perfect knowledge” of ancestry put to work: knowledge provided the capacity to wield selection and hybridization effectively.

East did not limit this combination of experiment and theory to only breeding

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<sup>593</sup> Shull, “The Genotypes of Maize,” 246.

<sup>594</sup> East and Hayes, *Heterozygosis in Evolution and in Plant Breeding*, 243:38.

<sup>595</sup> East and Hayes, 16, 21. East and Hayes were unsure of how useful inbreeding would be in general, pointing to effort, cost, price, and biology as determining the method’s value (pp. 47–48).

<sup>596</sup> East and Hayes, 32. Another formulation: “Crossing produces heterozygosis in all characters by which the parent plants differ. Inbreeding tends to produce homozygosis automatically.”

<sup>597</sup> Shull, “The Genotypes of Maize,” 252.

practices, again returning to a dissolution of distinctions between artificial and natural scenarios. He rejected the claim from biologists that successfully self- or close-fertilizing species were physiologically unique from those that cross-fertilized, a bias resulting from “the experimental breeder” witnessing the origin of and allowing degenerate strains. Cross-fertilized species, in fact, “produce strains poor in natural vigor, degenerate strains, and they are kept from sight.” Indeed, degenerate domesticated strains

survive the scythe of natural selection; they are selected for propagation by man because they are crossed with other strains and are vigorous through heterozygosity. Inbreeding tears aside their mask. They must then stand or fall on their own merits. Those strains with a high amount of natural vigor, due to gametic constitution, lose the added vigor due to a heterozygous condition, but are still good strains, ready to stand up forever under constant inbreeding. The poor strains that have had the help of hybridization with good strains, combined with the added vigor due to heterozygosity, are stripped of all pretense, shown in all their weakness, and inbreeding is given as the cause for their degeneracy. At least inbreeding has until recently been given as the cause, but it is hoped that the newer interpretation will now be accepted as logically interpreting all the facts.<sup>598</sup>

East and Hayes claimed that this theory of evolution and breeding extended to animals, writing that it was “speculative evolutionary philosophy” to declare sexual reproduction a “protoplasmic necessity.”<sup>599</sup> First-generation sterile hybrids seemed especially vigorous, although it was possible this was due to the elimination of the sexual organs (a trade-off). More importantly, while it was commonly believed that nature abhorred incest, “the greatest breeds of horses, cattle, swine, and sheep have been developed by in-and-in breeding.” In his early experiments with *Drosophila*, Castle had shown inbreeding functioned as it did in plants — it isolated homozygous strains without necessarily degenerating them. Thus, East and Hayes expanded their interpretations

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<sup>598</sup> East and Hayes, *Heterozygosis in Evolution and in Plant Breeding*, 38.

<sup>599</sup> They concluded that sexual reproduction is “not the cause of variation” and “presumably never increases variation.” Its role, instead, was to “permit recombination of the gametic factors of the parents, and this has no doubt been of great service in evolution.” For example, “if a rigid competition is allowed, new and better combinations of characters would replace the old.” East and Hayes, 44. Their conclusion was that sexual reproduction, or cross-fertilization, were byproducts of heterozygosis. They suggested that cross-fertilization may not be ultimately advantageous; that is, cross-fertilization allowed for “the survival of weak strains in combination.” Therefore, cross-fertilization and self-fertilized species were not necessarily weaker or stronger than the other. East and Hayes, 45.



beyond crops to animals and nature.<sup>600</sup>

Still, East emphasized how much work remained. “When one speaks of producing new plants, ... he should not be misunderstood. Man has not yet actually produced new variations (although the time may come when even this is possible); he simply works with the variations which have occurred through natural causes of which little is known.” In hopes of creating mutations, East was excitement for MacDougal’s (CIW-funded) injection work. He reasoned that the method was worth pursuing because “progressive variation occurs but rarely in nature,” so “one ought then to expect to increase this proportion only if he can multiply artificially the effectiveness of nature’s causes.”<sup>601</sup> He reported negative results in his own attempt to turn a yellow tomato red, but as with MacDougal’s work, East emphasized that well-done experiments that gave negative results to control evolution were still worth reporting.

But it was this point around 1912 that East and Shull concluded their engagement in debates in experimental evolution. Their development of pure line theory, its incorporation into genetics through homo- and heterozygosity, and East’s co-articulation of multiple factors were essential contributions to the science of evolution.<sup>602</sup> Although

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<sup>600</sup> East and Hayes, *Heterozygosis in Evolution and in Plant Breeding*, 38, 40.

<sup>601</sup> East, “Notes on an Experiment Concerning the Nature of Unit Characters,” *Science* 32 (1910): 93–94. He proposed injecting plant embryos with enzymes from different species. He also discussed MacDougal in *Report of the Connecticut Agricultural Experiment Station for the Years 1907-1908* (Hartford: State of Connecticut, 1908), 433. Shull made similar remarks about MacDougal in 1907.

<sup>602</sup> One article worth remarking upon however is East and Hayes, “A Genetic Analysis of the Changes Produced by Selection in Experiments with Tobacco,” *American Naturalist* 48 (1914): 5-48. In cooperation with the Connecticut Agricultural Experiment Station and the Bureau of Plant Industry, they sought to extend the pure line work to the crossbreeding crop, tobacco. They intended to show that genetic responses to selection, contrary to Castle, should be “interpreted entirely by the segregation and recombination of hypothetical gametic factors which are constant in their reactions under identical conditions.” Simultaneously, the work also shows the tension between understanding evolution in the wild versus evolution in a crop field. Their experiment crossed two tobacco varieties that differed in leaf number and selecting the extremes in both directions. (By doing so, they showed that a specific and profitable tobacco strain named “Halladay” was a reproducible hybrid between “Havana” and “Sumatra,” not a mutation.) After selfing 100 Halladay individuals, they selected for higher or lower leaf numbers in the 100 families with population sizes in the several hundreds. They found that consistent with the Mendelian-mutationist argument, the 100 families differed in how they responded to selection in terms of final leaf count and how long it took to reach that point. They thus demonstrated the genetic variation within their populations of tobacco and selection’s limitation to what was available. They also figured that while selection could “always cause a shift in the mean ... it will necessarily be ... so slight that it can be detected only by long-continued experiment and enormous numbers”: perhaps relevant for evolution in the wild, but not so much for “experimental genetics.” East and Hayes concluded that “important economic results can be obtained easily and surely by selection” by “the isolation of homozygous strains from mixtures that are either mechanical or physiological, that are either made artificially or are found in nature.” They also notably

they no longer personally participated in the ensuing debates, Castle's opponents adopted their work enthusiastically and transformed them into the orthodox view. Castle himself rejected the universality of their ideas, if not totally, partially due to the implications for control. For what Shull had said in 1907 seemed to remain to be the case: "we seem to be at present entirely at the mercy of nature" but perhaps "ready to take advantage of and preserve every advance she makes." But it was this view that Castle could not abide.<sup>603</sup>

### Castle's Theory of Selection as a Sliding Scale

In 1911, Castle reiterated his goals of controlling evolution. In a lecture, he said,

The evolutionary idea has forced man to consider the probable future of his own race on earth and to take measures to control that future, a matter he had previously left largely to fate. With a realization of the fact that organisms change from age to age and that he himself is one of these changing organisms, man has attained not only a new ground for humility of spirit but also a new ground for optimism and for belief in his own supreme importance, since the forces which control his destiny have been placed largely in his own hands.<sup>604</sup>

For these lectures, however, Castle was not so much interested in the destiny of human evolution, but in controlling the evolutionary improvement of livestock. Believing that civilization and its future progress rested upon the cultivation of domesticated plants and animals, a scientific understanding of breeding was critical. According to Castle, the issue at hand remained *how*.

... the production of new and improved breeds of animals and plants is historically a matter about which we know scarcely more than about the production of new species in nature. Selection has been undoubtedly the efficient cause of change in both cases, but how and why applied and to what sort of material is as uncertain in one case as in the other.<sup>605</sup>

Castle continued to pit selectionism against mutationism within this context of

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challenged some tenets of de Vries' mutation theory, an example of how the integration of Mendelism *sublated* (but did not entirely overthrow) mutationism.

<sup>603</sup> Shull, "Importance of the Mutation Theory in Practical Breeding," *Journal of Heredity* 3 (1907): 65.

<sup>604</sup> Castle, *Heredity in Relation to Evolution and Animal Breeding* (D. Appleton, 1911), 1–2. These originated as lectures (one of which Sewall Wright attended), later published as a standalone book and the second as a chapter within a volume with contributions from East, Tower, and Davenport on evolutionary science's latest findings.

<sup>605</sup> Castle, 3–4.

control. He described the latter as “the way in which Minerva was begotten.” Darwinian selection, on the other hand, was akin to “the ever-growing power of a hydraulic press.”<sup>606</sup> Mutations were responsible for some changes, such as “the great color variation of domesticated animals” resulting from the “accidental loss of simple unit-characters.”<sup>607</sup> But, as with Minerva’s birth, these mutations remained outside of human control, and lacked creative power, whereas selection was not only under direct human control, but became more powerful as it accumulated variations (the “hydraulic press”).

Castle contrasted his own work with that of de Vries, Johannsen, and Jennings, critical of both mutationism and pure line theory. Castle worried that through the “brilliancy of Mutation theory,” de Vries “has somewhat dazzled our eyes” regarding the “efficacy of selection.”<sup>608</sup> Castle compromised, saying selection was slower to work within a pure line than in a “mixed race,” but asked, “we know the effects should be *less*, but are they *nil*?”<sup>609</sup> It was the pure line workers’ absolutism with which Castle took umbrage.

Castle also rejected East’s multiple factor theory, remarking that selection would then become “*dependent upon* the inheritance of unchanging units,” increasing or decreasing the proportions of two or three characters “until a pure race was obtained.”<sup>610</sup> He claimed his study of hooded rats had shown instead that “these quantitative variations behave as *simple* units, not as multiple ones ... The only logical escape from this dilemma for one devoted beyond recall to a pure-line hypothesis will be to assume further that the assumed multiple units are all coupled ... so that in cell-division they *behave* as one unit.”<sup>611</sup> Moreover, a collection of unchanging units, according to Mendelian theory, would require breeders to carry out crosses with an immense number of offspring in order

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<sup>606</sup> Castle, “The Method of Evolution,” in *Heredity and Eugenics* (Chicago: The University of Chicago Press, 1912), 39–40.

<sup>607</sup> For example, the wild house mouse by simple loss of three independent factors has given rise to seven additional varieties known among fancy mice.” Castle, 52–53. (A “unit-character” was a trait that segregated.)

<sup>608</sup> He once again cited de Vries’ buttercup experiments as corroborating his own. De Vries had concluded that increased petals was a Mendelian unit-character produced by mutation and that after five generations, selection’s ability to increase petals had been exhausted; however, Castle argued that there should have been no further increases following two generations if Mendelism fully explained the results. Castle, *Heredity in Relation to Evolution and Animal Breeding*, 107–11.

<sup>609</sup> *Ibid.*, 117.

<sup>610</sup> Castle, “The Method of Evolution,” 55–56. Emphasis mine.

<sup>611</sup> Castle, “The Inconstancy of Unit-Characters,” *The American Naturalist*, 1912, 359.

to produce all possible genetic combinations.<sup>612</sup> A theory of a single quantitatively varying factor subject to selection was simpler to put into practice.

To counter the pure line and multiple factor theories, Castle reiterated his own theory of creative selection and gametic contamination along with the introduction of “potency,” now “of prime importance in evolution.” Castle developed the concept from his polydactylous guinea pigs, whose extra digit’s relative potency, or perfection, varied and was inherited among individuals in non-Mendelian proportions. While he acknowledged that the extra digit, and potency in general, could be explained by “several independent factors,” he considered it improbable (but testable).<sup>613</sup> Instead, “this manifestation of the character, though feeble, was sufficient to afford a guide for selection of those individuals which formed the most potent gametes, and so a polydactylous race was formed by selection and inbreeding.”<sup>614</sup> Selection now also accounted for the role that Castle previously gave to mutation.

Castle elaborated upon how his hooded rats demonstrated the creativity of natural selection, introducing an important theory about its action (or inaction) on variability:

The amount of variability of the offspring is not materially affected by the selection, but the average about which variations occurs is steadily changed, as are also the limits of the range of variation. The interesting feature of this experiment is the production, as a result of selection, of wholly new grades [in both directions]. ... By selection we have practically obliterated the gap which originally separated these types... Regression grows less with each successive selection and ultimately should vanish, if the story told by these statistics is to be trusted. As yet there is no indication that a limit to the effects of selection has been reached.<sup>615</sup>

Castle argued that selection, moving the mean of a trait in one direction, facilitated new

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<sup>612</sup> Breeding tests could ensure purity, but the exertion required made it less practical than simply eliminating the homozygous recessives across generations. Castle, *Heredity in Relation to Evolution and Animal Breeding*, 47.

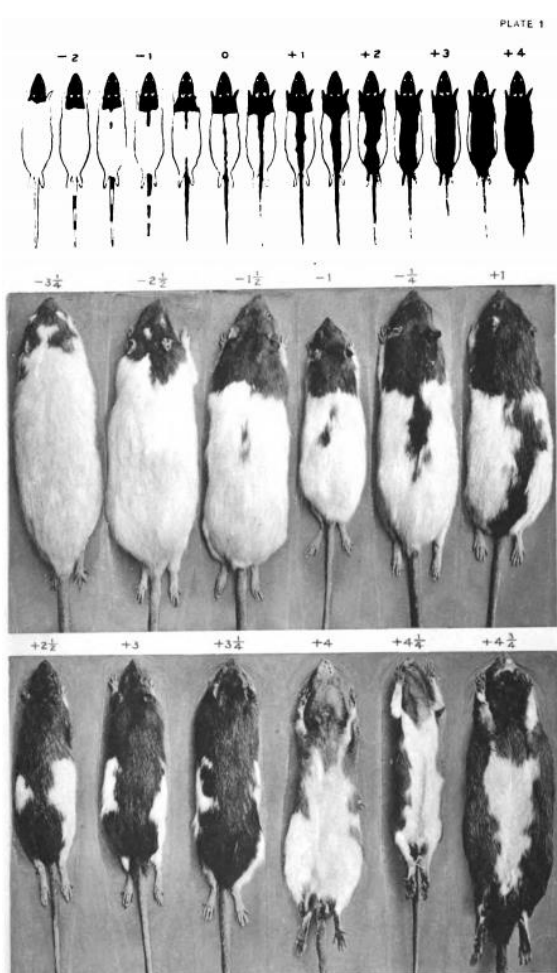
<sup>613</sup> Ibid., 100–101. He still followed Mendelian thought here in that he considered potency a property of a unit character, not of a gamete or individual (apparently in contrast to the breeders). Alfred Sturtevant later remarked that Castle never tested it; therefore, the polydactylous guinea pigs could not be considered evidence in favor of gametic contamination (discussed below).

<sup>614</sup> Castle, 104. Castle used nearly identical language in “The Method of Evolution.” To bolster the concept of potency, Castle cited the work of Richard Woltereck on parthenogenetic (pure line) water fleas (*Hyalodaphnia*). According to Castle, Woltereck’s selections had “served to augment both the degree of development of an organ [a rudimentary eye made of pigmented cells] and the frequency of its occurrence within that race (Castle, *Heredity in Relation to Evolution and Animal Breeding*, 97–98.)

<sup>615</sup> Castle, “The Method of Evolution,” 60–61.

variations farther along the spectrum, rather than reducing variability. Thus, Mendelism, while a “great contribution,” did not supply the whole foundation of evolutionary control.<sup>616</sup> Although Castle never used this term, Morgan later designated this theory the “sliding scale,” a term I adopt for clarity. In his words, selection, under Castle’s interpretation, “could slide successive generations along in the direction of selection.”<sup>617</sup>

Figure 6: From Castle and Phillips, *Piebald Rats and Selection* (1914), Plate 1.



visible changes witnessed in real-time, not random mutations. Indeed, despite the protests of pure line workers, who believed “selection can do nothing but sort out variations already existing in a race,” Castle asserted “*there are strong reasons for believing that mendelizing [sic] characters can be modified by selection.*” While mutations did occur, “more frequent and more important, probably, are slight, scarcely noticeable modifications of unit-characters that afford a basis for a slower alteration of the race by selection,” interpreted as “slight differences in the potentiality of gametes representing the same unit-character combinations.” Therefore, Castle “prefer[red] to think with Darwin ... that [selection] can

<sup>616</sup> Castle, *Heredity in Relation to Evolution and Animal Breeding*, 104–5. This can also be seen in how Castle subordinated Mendelism to potency: Castle found that the starker the difference between the dominant and recessive traits, the more Mendelian it behaved in crosses. He concluded that the degree of difference depended upon the relative potency of the two characters, conditional upon the environment (pp. 97–98).

<sup>617</sup> Thomas Hunt Morgan, *A Critique of the Theory of Evolution* (Princeton: Princeton University Press, 1916), 153–55. See John Beatty, “The Creativity of Natural Selection?”, 672.

heap up quantitative variations until they reach a sum total otherwise unattainable, *and that it thus becomes creative.*"<sup>618</sup>

Castle had continued his long-term experiments, raising and grading 25,000 rats over 13 generations by 1914, the results further confirming his theoretical interpretations. (See Figure 6.) Working with student John C. Phillips, he continued their plus and minus selection experiments on pigmentation, alongside reverse experiments and crosses.<sup>619</sup> In the five generations since his 1911 book, selection respectively widened and narrowed the stripes of the plus and minus series.<sup>620</sup> Variability had decreased, but on account of large generation sizes allowing for "more rigid selection." Regression toward the mean persisted, but decreased in magnitude as the means increased.<sup>621</sup> Hence, selection was a sliding scale.

Castle's sliding scale theory could also account for mutations. When he discovered two possible mutants in the plus series, he suggested that it "seems to us quite improbable that the plus mutation could have arisen in the minus selection series." Rather, "we believe that the repeated selection which was practised had something to do with inducing this change in the plus direction." According to Castle, the Mendelians were wrong: mutations were under the ultimate direction of selection, not the other way around.

Having demonstrated that one can increase and decrease pigmentation "at will" in a single direction, it remained open whether such changes were permanent and whether selection's accumulation could be *reversed*. Castle and Phillips found that during return selections, the direction of regression itself reversed, *away* from zero, "toward the mode established by selection," producing new centers of variation. These results confirmed that selection was "*immediately effective*" and "has cumulative and permanent effects."<sup>622</sup>

Although Castle admitted that multiple factor theory made sense of some results,

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<sup>618</sup> Castle, "The Method of Evolution," 56, 61. In the 1911 publication, but not in the 1912 version, Castle also included in his conclusion that: "It is possible to ascribe such differences to little units additional to the recognized larger ones, but if such little units exist, they are indeed very little as well as numerous, and by adding to the effect of the larger ones they produce what amounts to modification of them" (pp. 126-127).

<sup>619</sup> Castle and John C. Phillips, *Piebald Rats and Selection: An Experimental Test of the Effectiveness of Selection and of the Theory of Gametic Purity in Mendelian Crosses* (CIW, vol. 195, 1914).

<sup>620</sup> Castle and Phillips, 195:37, 43.

<sup>621</sup> Contrary to the pure line theory, which held that regression should be complete.

<sup>622</sup> Castle and Phillips, 14-15, 16, 22.

he rejected it in favor of selection's creativity. The theory was consistent with increased variability in the generation following a cross (maximum heterozygosity) as well as selection decreasing that variability over time (reduction of heterozygosity). But with the total loss of variability being minimal, Castle believed the endpoints — all black and all white rats — remained within selection's reach. He also did not think the theory would alter selection in practice. If modifiers were to spontaneously appear, "selection can use these to modify the pattern ... [and] we must admit that selection is an agency of real creative power." It was the force that could "secure at will" change in any direction.<sup>623</sup>

### Castle's Battle with the Pure Line Work and Multiple Factor Theory

At this point, extensive debates erupted among the experimental evolutionists on numerous argumentative fronts against Castle. I first address the disputes between Castle with H. J. Muller and the Hagedoorns that revolved around the "fundamentality" of pure lines, both methodologically and theoretically, as well as selection. I then turn to his debate with Raymond Pearl which offers an interesting look at the notion of populations at the time. Despite the full-out attack, Castle remained steadfast in his views.

Castle rejected the pure line theory as non-scientific. He even compared the pure line workers to geometers, as opposed to those rooted in practice such as breeders and draftsmen:

The biologist's "pure line" is an imaginary thing. I doubt very much whether it was ever realized in any actual race of animals or plants. It has no more relation to actual animals and plants than a mathematical circle has to the circles described by the most accomplished draftsman. All the circles of the draftsman have wiggles in them, if you look at them carefully enough; only the mathematician's imaginary circle is perfect. Now the biologist undertakes to be the mathematician of breeding and to construct an "exact" system of heredity in which the "pure line" concepts holds a conspicuous place.<sup>624</sup>

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<sup>623</sup> Ibid., 23–26.

<sup>624</sup> Castle, "Pure Lines and Selection," 93. "Exact" is a reference to Johannsen's book. Castle's accusation of idealism ironically ignores the dialectical interplay of mathematical theory and practice. Marga Vicedo has also analyzed the Castle's debate (specifically with East) and highlights that rhetoric around realism/idealism and complexity/ simplicity was mostly to score argumentative points, rather than substantial critiques, in "Realism and Simplicity in the Castle-East Debate on the Stability of the Hereditary Units: Rhetorical Devices versus Substantive Methodology." *Studies in the History and Philosophy of Science* 22 (1991): 201-221.

Like geometry, Castle argued the pure line theory was deduced from two assumptions: that “the effects of the environment are not inherited” and “inherited characteristics [specifically, “factors”] do not vary.” Castle agreed that experimental evidence, including his own work on ovary transplantation, confirmed the first, rejecting neo-Lamarckism. He attacked the second, however, using his own experimental cases while questioning those of his opponents. He argued that constancy should be attributed to traits, not to their “ultimate factors of inheritance,” and assuming such was to treat genetic factors like the imaginary “circles of the mathematician.”<sup>625</sup> Castle elaborated upon this accusation of idealism, insinuating that even if one could remove all environmental effects and modifying factors, any sign of variation would cause a pure line worker to “suppose that all factors but one have not yet been eliminated.”<sup>626</sup> Moreover, Johannsen and Jennings based the theory on size characters, continuous traits without a proved Mendelian basis (even if one included “hypothetical” modifying factors). Castle wrote, “this is like supposing that the moon is made of cheese and that further this cheese is *green*.”<sup>627</sup> When responding to Muller’s claim of pure line theory’s fundamentality (below), Castle again remarked on the “slender basis” in which Mendelism and pure line theory had become entangled, asking “do biologists take themselves seriously when they reason thus?”<sup>628</sup>

Throughout the 1910s, Castle faced several attacks from the Dutch animal breeders, Arend and Anna Hagedoorn, the up-and-coming *Drosophila* geneticist Hermann J. Muller, his former student, E. C. MacDowell, and Raymond Pearl, who had worked out pure line theory in poultry.<sup>629</sup> These attacks took every available path, including

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<sup>625</sup> Castle, “Pure Lines and Selection,” 94. On this point Castle was not totally unique; Bateson and Morgan, among others, had their own skepticism of genes that changed over time.

<sup>626</sup> When Johannsen “was successful, he attribute[d] the success to variation in genetic factors; whenever unsuccessful he assumes that no variation in genetic factors occurred.”

<sup>627</sup> Castle, 95.

<sup>628</sup> “We shall look in vain, I think, for those “principles” outside of the “*Exakten Erblchkeitslehre*” (or its imitations), and when we inquire as to the experimental basis of the principles in question we are met with the satisfied reply, “Johannsen’s beans.”” Castle, “Mr. Muller on the Constancy of Mendelian Factors,” *The American Naturalist* 49, (1915), 40. Hermann J. Muller, “The Bearing of the Selection Experiments of Castle and Phillips on the Variability of Genes,” *The American Naturalist* 48 (1914): 568. Muller explained Castle’s crossing experiments by assuming that wild and Irish rats contained numerous ‘plus’ modifying factors (as Castle suggested).

<sup>629</sup> For more on Arend Hagedoorn, who was a student of de Vries and Loeb, see Bert Theunissen, “Practical Animal Breeding as the Key to an Integrated View of Genetics, Eugenics and Evolutionary Theory: Arend L. Hagedoorn (1885–1953),” *Studies in History and Philosophy of Science Part C: Studies in History and Philosophy of Biological and Biomedical Sciences* 46: 55-64 (2014).



methodological, presentative, theoretical, and practical critiques. This section summarizes the most pertinent exchanges regarding the interaction of genetics with “the selection problem.”<sup>630</sup>

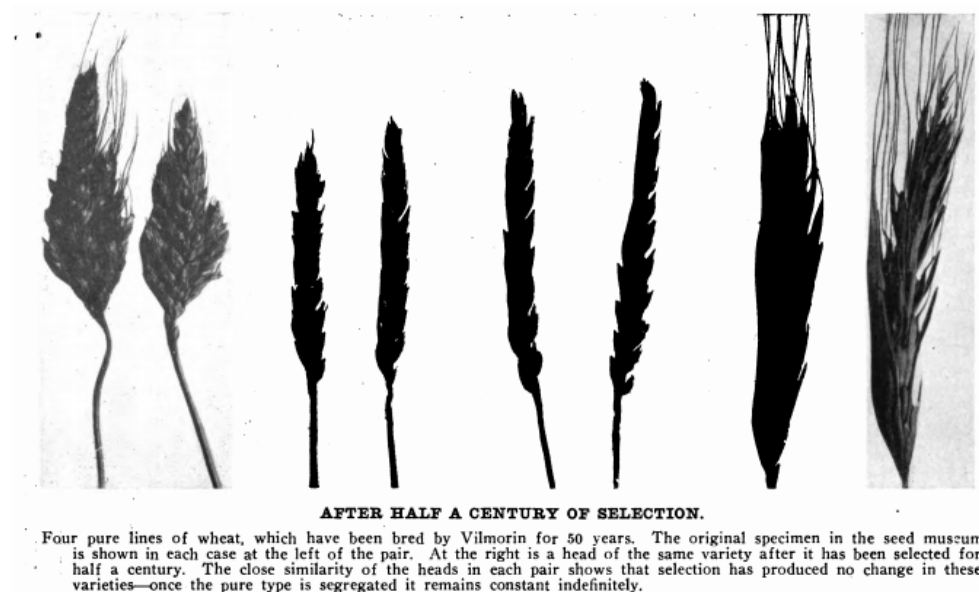


Figure 7. From “Selection in Pure Lines” (1913).

The Hagedoorns used a “natural experiment” to challenge Castle, work he considered hypocritical. They compared contemporary wheat to plants in Louis de Vilmorin’s “living museum of pure lines of commercial wheats,” claiming that “fifty years’ work in wheat ... show[ed] not one of the varieties changed in any way by these generations of selection.” Therefore, “selection can have no effect in material pure for its genetic factors. Genetic factors are constant.”<sup>631</sup> (See Figure 7.) But Castle noted, they did not depict the entire wheat plant, ignored potential physiological changes or limits, and neglected to discuss whether Vilmorin selected *to type* (no expected change) or *to change*

<sup>630</sup> The cited critiques and responses are worth further investigation as commentaries on the contemporary state of genetics and experimental evolution.

<sup>631</sup> Hagedoorn and Hagedoorn, “Selection in Pure Lines: Fifty Years’ Work in Wheat by Vilmorin Shows Not One of the Varieties Changed in Any Way by These Generations of Selection,” *American Breeders’ Magazine* 4 (1913): 167. This was not to say that selection was ineffective within a population. For example, the Hagedoorns adopted a dynamic model similar to East and Shull, claiming that “animal populations are nearly always impure for the most diverse genetic factors,” whether wild or domesticated, making selection usually effective (unless highly inbred), but to a limit, speed depending upon the degree of genetic mixture. Hagedoorn and Hagedoorn, “Studies on Variation and Selection,” *Zeitschrift Für Induktive Abstammungs- Und Vererbungslehre* 11 (1914): 155–56.

the type. They also challenged opponents to use selection to change a character after inbreeding and then reverse it while accounting for genetic “impurities.” Castle noted they had not rose to the challenge themselves and maintained that he had already met theirs, claiming also that fifteen generations of selection should have eliminated the original variation.<sup>632</sup> He posed a contrary challenge, that selection on “any character of any animal” would prove its effectiveness.<sup>633</sup> Most breeders had themselves shown this already, according to Castle, because pure lines are “purely imaginary.”<sup>634</sup>

The Hagedoorns lodged a more serious theoretical and methodological critique, however, echoed by Muller and Pearl: Castle assumed an identity between genotype and phenotype, ignoring that a phenotype could be produced by multiple genotypes or by the environment. Castle, for example, argued that “in this series of rats the somatic character (appearance) of an individual is in general a true indication of its germinal character, since the higher the grade of the parents the higher the grade off the offspring, and *vice versa*.”<sup>635</sup> This assumption “decimated the value of his work,” according to the Hagedoorns, because more than one gene could be producing the same character.<sup>636</sup> In essence, Castle’s selections may be associating or eliminating independent factors, not changing a single gene or “unit-character.”<sup>637</sup> Castle’s rats may in fact be “a complete analogon to Nilsson-Ehle’s case of the coloured wheats.” The Hagedoorns therefore flipped Castle’s assertion that size may not be Mendelian against him.<sup>638</sup>

The Hagedoorns also pointed to a statistical methodology that neglected biological causes. Reminiscent of Bateson’s criticism of Weldon and Pearson, the Hagedoorns bounced back the geometer insult and accused Castle of being a

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<sup>632</sup> Castle, “Variation and Selection; a Reply,” *Molecular and General Genetics MGG* 12 (1914): 259.

<sup>633</sup> They soon conducted their own experiment with hooded rats which ended prematurely after three years due to an “all-devastating epidemic,” but still concluded there were at least two genes responsible for the trait. (They further claimed to have achieved “far better results than Castle” due to their strict inbreeding and rigorous selection.) Hagedoorn and Hagedoorn, “Studies on Variation and Selection,” 165–70.

<sup>634</sup> Castle, “Pure Lines and Selection,” 97.

<sup>635</sup> Castle and Phillips, *Piebald Rats and Selection*, 12.

<sup>636</sup> “The possibility remains, that amongst [Irish and hooded rats], more than one gene differentiates the animals, and that selection favours a change of proportion between animals with and those without such genes.”

<sup>637</sup> Hagedoorns, 162-163. Specifically, they claimed that there may not even be a “main” factor that was modified by other factors; instead, the trait may be entirely built by independent factors, even if some had more of an influence than others. In fact, the Hagedoorns considered the multiple factor theory as “not a new one at all,” but made to “look new” by the incorrect “one-factor-one-character idea” (p. 181).

<sup>638</sup> Hagedoorn and Hagedoorn, 163.

mathematician himself, “absolutely callous to the biological problems involved, delighting in arranging and manipulating the figures for their own sake ... hopelessly tangl[ing] up ... causes.” Instead, “for the biologist the statistical method must be the very last resource.” Statistical methods based on appearance assumed genetic homogeneity and could not account for modifying factors or environmental effects. As MacDowell put it, Castle measured “one variable (germ plasm) through a measure (soma) influenced by a second variable (environment),” the last of which “of [its] power and nature nothing seems to be known.” Thus, in addition to modifying factors, MacDowell suggested that Castle may have witnessed strong environmental influences producing high variability, “confus[ing] the various combinations of germinal factors, and selection would continue to produce slight advances for a long time,” the same problem that Jennings had encountered in 1908. The problem, according to MacDowell, as well as the Hagedoorns, was that Castle extended his arguments beyond the phenotypic effects of selection to the “nature of the changes in the germ plasm.”<sup>639</sup> This specific argument is what the *Drosophilists* would later focus upon (discussed below).<sup>640</sup>

Muller elaborated on the point of multiple factors through a reinterpretation of Castle’s experiments. Although Castle had argued that fifteen generations of selection were sufficient to eliminate his stock’s heterozygosity, Muller suggested that the rats remained “presumably heterozygous.” If there was a high enough number of factors contributing to coat color, then Castle’s advances and reversals remained possible. Unlike *Drosophila*, in which genetic factors could be closely followed, Castle’s experiment on the hooded rats in itself could not address the underlying genetic and chromosomal mechanics. Rather, Castle’s results were consistent with Johannsen, who had “proved the

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<sup>639</sup> MacDowell, “Piebald Rats and Multiple Factors,” *The American Naturalist* 50 (1916): 722. MacDowell listed over ten points in favor of the pure line and multiple factor theories, some of which Pearl, Muller, and the Hagedoorns had articulated. Castle believed he had already successfully countered them and admonished MacDowell for failing to explain how the data was equally compatible with Castle’s interpretations: Castle, “Piebald Rats and Multiple Factors,” *American Naturalist* 51 (1917): 103

<sup>640</sup> On causes, the Hagedoorns even indirectly accused Castle of Lamarckism for his sliding scale theory: that selection itself is responsible for producing adaptive variations. Instead, selection could alter “the mean of the group”; that “selection can not influence a gene” was a “law” “to which there are no exceptions.” Hagedoorn and Hagedoorn, “Studies on Variation and Selection,” 182. Beatty touches on this argument implicitly with respect to Morgan and de Vries: “The question as to how variations arise should be kept separate from the question as to whether they will be selected or not.” Beatty, 676.

constancy of a great many genes ‘at one blow.’”<sup>641</sup> (By this Muller meant that because size was the result of multiple factors, and Johannsen had shown the constancy of size, then this meant that the “great many genes” were also constant. Castle specifically rejected this argument.) Multiple factors also explained the blending in the offspring of the plus and minus cross as well as the decreased variability upon return selection, as “selection gradually tends towards homogeneity in a population.”<sup>642</sup> Therefore, Castle’s results were due to mixes of existing factors.<sup>643</sup> That Castle rejected this Mendelian interpretation in favor of his theory of gametic contamination irked Muller, who suggested that Castle was taken in by a “spirit of mysticism.”<sup>644</sup>

Castle, unperturbed, continued his attacks on the pure line theory and factor constancy in favor of his version of Darwinism in experimental systems outside the hooded rats. In a genetic study of color patterns in rabbits, he found that repeated crossing between two Mendelian traits caused the independent “English” pattern to darken. This provided “conclusive evidence against the idea of unit-character constancy,” in favor of gametic contamination, allowing him to assert that “if unit-characters are not constant, *selection reacquires much of the importance which it was regarded as possessing in Darwin’s scheme of evolution*, an importance which many have recently denied to it.” In another case, a newly discovered allele of agouti in rabbits, “black-and-tan,” afforded him the possibility to test for the presence of modifiers using the Drosophilists’ linkage theory. According to linkage theory, the likelihood of the two genetic factors breaking apart increased with the number of crosses, but no evidence of this appeared. Instead, “the present modal condition of the black-and-tan character is one which has been attained only as a result of persistent selection,” amenable to “gradual and apparently indefinite modification.” Not only were there likely more alleles for

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<sup>641</sup> Muller, 574. The Drosophilists asserted that Castle’s hooded rats were “a good illustration of the effects of selection on a group in which a particular character owed its modifications to multiple factors.” Morgan, et al., *The Mechanism of Mendelian Heredity* (Holt, 1915), 201–2.

<sup>642</sup> Muller, “The Bearing of the Selection Experiments of Castle and Phillips on the Variability of Genes,” *The American Naturalist* 48 (1914): 572. Muller contradicted the Hagedoorns due to the fact that he had to acknowledge Castle’s success with return selections.

<sup>643</sup> MacDowell, discussed below, reinterpreted a case of “genic variation and contamination” to be a case of selection of constant multiple factors, pointing against Castle’s interpretations. Muller, 576.

<sup>644</sup> Castle’s theory of gametic contamination “violat[ed] one of the most fundamental principles of genetics—the non-mixing of factors—in order to support a violation of another fundamental principle—the constancy of factors.” Muller, 573–575.

experimental breeders to reveal, but the two cases showed that breeders' own selection could modify these factors. Castle concluded, "here are fruitful fields of inquiry to be cultivated before we conclude with the exponents of 'exact' heredity that selection of fluctuations is useless and that only mutations count in evolution."<sup>645</sup>

Strangely, as Castle worked with chromosomal mechanics (such as linkage) in these two cases, he also diminished its importance, returning to practice. Castle wrote, "whether an imaginary 'unit-factor' for English pattern has or has not changed in correlation with the visibly changed English unit-character" was only of "academic interest." It "scarcely affect[ed] the *practical question* whether the visible Mendelizing characters of animals are subject to change through crossing or through selection or both."<sup>646</sup> The difficulty of assessing the existence of a modifier next to black-and-tan rendered it "unimportant." What mattered was that selection caused evolutionary change, not the underlying mechanics. He concluded in another paper that East's and Nilsson-Ehle's multiple factor theory was "quite superfluous."<sup>647</sup>

Raymond Pearl, too, entered the fray, debating with Castle on the nature of selection's interaction with characters and populations, through both methodological and theoretical grounds. Raymond Pearl elaborated and extended the arguments that "*selection can change a population but not a character.*"<sup>648</sup> He argued that both Castle's work and his own work with poultry had demonstrated this principle. Castle believed Pearl was comparing apples to oranges. Whereas Castle dealt with a visible, developmentally early, and sexually universal trait, Pearl experimented with winter egg production, a sex-linked physiological trait that appeared only upon sexual maturity. Although Pearl claimed that egg production was controlled by two genetic factors, he had not provided the data for others to independently calculate; thus, unlike color, but like

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<sup>645</sup> Castle and Philip B. Hadley, "The English Rabbit and the Question of Mendelian Unit-Character Constancy," *PNAS* 1 (1915): 42; Castle and H. D. Fish, "The Black-and-Tan Rabbit and the Significance of Multiple Allelomorphs," *American Naturalist* 49 (1915): 93–96. Emphasis mine.

<sup>646</sup> Castle and Hadley, 42. Castle had made the similar argument that whether traits were the result of a single gene or many genes of small effect, "selection slowly and surely changes the range of variability" ("Mr. Muller on the Constancy of Mendelian Factors," 39, 40).

<sup>647</sup> Castle, "New Light on Blending and Mendelian Inheritance," *American Naturalist* 50 (1916): 334. This article was a commentary on another article about the genetics of flowering time in peas. Castle consolidated the author's two-factor (four class) system into a single quantitatively varying factor.

<sup>648</sup> Castle, "Some Experiments in Mass Selection," 713.

size in Johannsen's beans, Castle did not grant that egg production was Mendelian. Disease, parasitism, crowding, and nutrition were harder to control in poultry-keeping, which hindered statistical sampling and limited the amount of "material on which selection can be practised." Rats, in contrast, aided sampling techniques and afforded selection "a vastly greater amount of material to work with."<sup>649</sup> Pearl's entire flock over seventeen years numbered 4,282 individuals, whereas Castle, at the time of writing, raised and measured 33,248 individuals over seventeen generations — the 16th plus selection produced 1,690 offspring alone, "numbers certainly more nearly justifying the term 'mass selection' than those studied by Pearl." Thus, "the hooded pattern of rats is materially admirably adapted for the purpose" of an "experimental test of "mass selection." Pearl's poultry, on the other hand, were "entirely unsuitab[le]."<sup>650</sup> On this point, Pearl explained that in addition to deaths, a major sampling effect took place every generation in both experimental systems. He also remarked that in total numbers, Castle's rats were dwarfed by the commercial and "expert" crop breeders, such as the "pioneer work at Svalöf"; the spread of its methods in cereal crops demonstrated as "fact, real and definite," the validity of the pure line theory and factor constancy. Castle conceded these methodological points but held fast to his theoretical commitment.<sup>651</sup>

Theoretical differences over the interaction of selection and variation were clarified through the exchange. Pearl's success with selecting between pure lines entailed that he had not produced a race superior than the original stock in terms of egg

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<sup>649</sup> Castle had noted this importance when attacking the Hagedoorns: when charged with inbreeding insufficiently, he pointed to the need to balance the needs of the experiment with the needs of his stock's vigor and survival. He slyly pointed out that had he followed the Hagedoorns' advice, his "experiments would have ended as abruptly as those of [his] critics," who had lot sizes as small as fifty-nine individuals and lasted only "two full selections," the last producing only six offspring. He later noted that "in the third and all subsequent generations selection was made as rigorous as possible consistent with the maintenance of a strong colony from which to make further selections." Castle, "Some Experiments in Mass Selection," *The American Naturalist* 49 (1915): 721. In 1916, Castle claimed were he to meet his critics' standards, his stocks would fail to produce enough offspring to sustain the population; even his own methods had "crossed the danger-line in advancing the standard of selection ...; more than once we have had to relax our standard temporarily in order to keep the race alive." Castle and Sewall Wright, *Studies of Inheritance in Guinea-Pigs and Rats*, 241 (Washington, D. C.: CIW, 1916), 168–169.

<sup>650</sup> Pearl was surprised by Castle's condescension. He conceded that Castle's "work on the selection is vastly superior to my own" and that his experiments "constitute[d] an achievement of which their author may well be proud." Unlike Castle, Pearl had focused only on differences of "interpretation," because Pearl admired "the factual basis afforded by" Castle's experimentation. Pearl, "Fecundity in the Domestic Fowl and the Selection Problem," *The American Naturalist* 50 (1916): 89–90.

<sup>651</sup> Pearl, 90–91, 100. Castle, "Can Selection Cause Genetic Change?," *American Naturalist* 50 (1916): 248–56.

production; instead, he had “secured” more of the better layers already extant within the stock. Castle, on the other hand, produced a stock wholly different than what had existed at the beginning, for “every individual” in either series “is of higher grade” — “a genuine and permanent racial change has occurred, following step by step upon repeated selection.” Castle felt “forced to conclude that this unit itself changes under repeated selection in the direction of the selection; sometimes abruptly...” and in either direction. (Hence the Hagedoorns’ accusation of Lamarckism.) In contrast to Pearl’s theory, “no great change in variability has attended the selection” of hooded rats, but instead, an increased mode and an entire shift of the trait’s distribution (the sliding scale). Pearl claimed that selection changed populations, but Castle believed, “in a word, the character changes.”<sup>652</sup>

According to Pearl, the combined results of commercial breeders and pure line workers demonstrated the “power of systematic selection to *alter populations* which were not pure lines” and that “such alteration may extend the range of variation very greatly beyond what it was in the original population.”<sup>653</sup> (As I have mentioned, this is signaling a transition to populational thinking.) However, a mutation, “a sudden definite change in the germ plasm” of any magnitude, was ultimately necessary. These mutational differences could be detected only through the cumbersome progeny test about which Castle complained, but, to Pearl, was one of the “chief results of the Mendelian method.”<sup>654</sup> This was especially critical, because as Castle himself knew as a collector of genetic anomalies, Mendelism entailed the existence of recessive allelomorphs, imperfect segregation, heterozygosity, and other conditions that prevented the biologist from assuming a simple 1:1 relationship between germ and soma. Coat color in rats may be a simpler trait than fecundity in poultry, but it was “a difference in degree, if they differ at all, not in kind.” Furthermore, this imperfect relationship meant that neither experimentalist had proved selection to be a cause in changing “the absolute somatic equivalent of a particular gene or hereditary determinant.” Castle, although altering the mean of a character within a population, could not demonstrate his argument by this

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<sup>652</sup> Castle, 722.

<sup>653</sup> Pearl, 100. Emphasis mine.

<sup>654</sup> Note that progeny tests preceded the rediscovery of Mendel, but Mendelism biologically explained its importance.

system alone.<sup>655</sup>

Pearl considered Castle's alternative theory to be "repugnant." The union of two gametes developing into a soma with a trait beyond the range of the parent population "leads logically straight to genetic indeterminism." Selection causing variation, Pearl considered a "nonsense" assumption, for it must result from hens being "placed in particular cages ... to breed, for this is the only physical thing that selection means in this case."<sup>656</sup> This produced a logical contradiction: how could selection *create* variation when breeding two genetically alike individuals especially when "as selection continues, homozygosity automatically increases"? Instead, Pearl said, "a new inheritable variation in the direction of selection *has appeared* while selection was in progress." The variation arose independently of selection: a mutation.<sup>657</sup>

Pearl charged that Castle's hypothesis was not Darwinism, but a "wholly new addition to the classic Darwinian selection theory," for "Darwin never supposed that selection was a cause of *favorable* variation." Indeed, if Darwin thought the source of variation was selection, why did he emphasize his own uncertainty? Although geneticists remained puzzled by mutation's causes, Pearl considered Castle's hypothesis "the rankest kind of mysticism plus bad logic."<sup>658</sup> Pearl hoped their differences "reduce[d] ... to a dispute over the use of words." He wished to convince selectionists not to use the formulation that 'selection causes new variation.'<sup>659</sup>

Whereas Pearl emphasized selection's tendency to reduce variation, Castle asserted that genetic variation was so widespread and available that a pure line likely never existed. Rather than "begging the question," Castle suggested that if two individuals of the highest grade reproduced, by chance, a small percentage could be of a

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<sup>655</sup> Pearl, 93, 100–101.

<sup>656</sup> Oddly, Pearl's symbolic example he used to work this out assumed a perfect relationship between germ and soma.

<sup>657</sup> Pearl, "Fecundity in the Domestic Fowl and the Selection Problem," 101–3.

<sup>658</sup> Pearl, 103–4.

<sup>659</sup> Pearl also pointed out that Castle's "special bete noir" remained his unfounded complaint that "pure-linists" deny the possibility of small "germinal variations." As Pearl's paper was published, Castle equated 'pure-linists' with nineteenth-century catastrophists and species fixists. To the contrary, Pearl said, correctly, that "neither Johannsen nor any followers of his, so far as I am aware, have ever attempted to set any limitations on how big or how little a germinal variation could be." Pearl, "Fecundity in the Domestic Fowl and the Selection Problem," 105; Castle, "Is Selection or Mutation the More Important Agency in Evolution?," *The Scientific Monthly* 2 (1916): 91, 98.



slightly higher grade than the parents – the causal basis of the sliding scale. Pearl had dismissed this “genetic indeterminism” as “repugnant” and “mystical,” but Castle interpreted this as “incapable of prediction and control.”<sup>660</sup> What was mystical was his opponents’ reliance on “*causeless* mutations” and “genetic miracles.” He concluded, emphasizing control,

Intelligent selection only accelerates this natural process of progressive variation, for it singles out the individual which is producing gametes of unusual value and permits the union of such high grade gametes only with gametes of their own sort, so that step after step in a particular direction becomes possible... Can we doubt that it is progressive variation guided by rational selection in a particular direction that has made possible the doubling in size that most of our domesticated animals have undergone since they were taken from the wild state?<sup>661</sup>

Rather than waiting for “causeless mutations” and “genetic miracles,” Castle could create the situation among his rats most likely to engender the selectable variation the breeder desired. He later pointed out that the pure line workers had to do the same if they were to wait for mutations to select.

Castle was careful to note the limitations of selection as well. For example, while Castle had failed to change the “mutants” with selection, he explained this away by pointing to the stock’s health: he struggled to raise enough mutant rats “to afford a basis for selection. Its inbredness and its feebleness are perhaps causally related.”<sup>662</sup> Therefore, selection’s ineffectiveness did not necessarily imply mutation’s importance. A further limit was that no character was capable of “indefinite modification” in every direction: sugar beets, for example, can hold only so much sugar and flies had only so much space for bristles. The slowing down of selection over time in some instances did not necessarily indicate the depletion of modifying factors; rather, selection run into physiological limits. This line of thought was in line with his early work on spotted guinea pigs.

Throughout these debates, Castle continued his experiments with hooded rats,

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<sup>660</sup> MacDowell also challenged this notion, discussed below.

<sup>661</sup> Castle, “Can Selection Cause Genetic Change?,” 248–49, 253–56.

<sup>662</sup> Castle and Wright, *Studies of Inheritance in Guinea-Pigs and Rats*, 241 (Washington, D. C.: CIW, 1916), 173.

now alongside his student Sewall Wright.<sup>663</sup> He had now graded over 33,000 rats through sixteen generations, evolution neither ceasing nor slowing.<sup>664</sup> The plus series now produced an individual “black all over except a few white hairs on the chest.” Variability remained “steady,” “plainly still large enough to permit further racial modification...” There was also “no indication that it will cease until the hooded character has been completely selected out of existence,” ending in all-black and all-white rats.<sup>665</sup> He held that sixteen generations should have eliminated any modifying factors that may have resided within the initial stock, thus, upholding his sliding scale theory. Furthermore, he claimed, extensive crosses between wild and domesticated guinea pigs confirmed it was a non-Mendelizing trait anyway. Where the multiple factor theory should have been the most helpful, a widespread continuously varying trait like size, it instead failed, being “quite unnecessary and so should be discarded.”<sup>666</sup> Instead, Castle’s single quantitatively varying factor, along with gametic contamination, was the simpler explanation, backed by his experimental systems as well as Jennings’ new work on *Diffflugia* (discussed below).<sup>667</sup>

But what mattered most to Castle was that the theory of varying factors and gametic contamination allowed for human control; the experimentalist, by selection, could direct future variation. In this context, Castle took the chance to challenge Galtonian theory (indirectly). He claimed that rather than remaining static and requiring a mutation to overcome, “points of racial equilibrium or stability” are “capable of being

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<sup>663</sup> In a collection of three reports published as one through CIW, Wright, sole author of the second report, established his career-long interest in physiological genetics and, contrary to Castle’s trajectory, espoused a pluralistic view, asserting that it was difficult to predict *a priori* what mode of inheritance a character will show, and that “in each case a complex of the most varied causes underlies an apparently simple continuous series of variations” produced by multiple allelomorphs, imperfect dominance, modifying factors, residual heredity, and non-inheritable effects. Castle and Wright, *Studies of Inheritance in Guinea-Pigs and Rats*, 120–21.

<sup>664</sup> Since the last report, the means of both the plus and minus series advanced a third of a grade in the parents and a fifth in the offspring.

<sup>665</sup> Castle and Wright, 170–71, 172.

<sup>666</sup> Castle and Wright, 55.

<sup>667</sup> He seems to have abandoned “potency” by this point. Castle offered an explanation of gametic contamination by way of metaphor: “if a 5 per cent solution of cane sugar were poured into the same dish with a 10 per cent solution and then samples were dipped from this before the two solutions had been thoroughly stirred together, it might very well happen that the samples would not be of uniform strength.” Because blending is imperfect, more variation should be expected in the offspring than in their inbred parents. This is why Mendelism explained the results of crosses between starkly differentiated hooded rats and Irish rats, but not between two alike selected hooded rats — contamination could not take full effect in the former in one generation. Castle and Wright, 55.

moved either up or down the scale of grades at the will of the breeder, provided he has the patience and persistency and will [to] select repeatedly.”<sup>668</sup> That is, his theory suggested a dialectic between the breeder’s selection and the internal constitution of the stock, rather than on the one hand, total control by the breeder, or on the other, total immutability from selection. As he concluded in his response to his former student, MacDowell,

But what happens to these spontaneous variations when once they have put in an appearance depends on external agencies, man or other factors in the struggle for existence. The modern study of evolution has indeed emphasized the importance of spontaneous internal changes in producing variations, but we still have to reckon with selection, natural and artificial, in determining the survival of variations as well as in controlling their magnitude and the direction of their further variation.<sup>669</sup>

Castle’s description of evolution was approaching his opponents’ with the language of “spontaneous internal changes” then becoming subject to “external agencies,” but he still emphasized selection’s power over mutation and variation – its creativity.

### **Jennings’ Conversion from Johannsen to Castle**

After his major 1908 publication on pure lines and selection, Jennings became director of the Zoological Laboratory at Johns Hopkins which under his direction published a number of “investigations on inheritance in uniparental reproduction ... to find heritable variations and effects of selection if such occur.”<sup>670</sup> To meet the standards of pure line critics, Jennings adopted a new organism, *Diffflugia*, and began a new series of long-term experiments testing the effectiveness of selection on a pure line. To his surprise, he discovered what he considered to be completely contrary to his accumulated years of evolutionary work: pure lines varied more than thought, thus making selection effective within a pure line. He published his new work in the first volume of *Genetics*, despite it not containing any Mendelism, showing the loose integration of experimental evolution and genetics.<sup>671</sup> Jennings was the only major defection from the pure line camp

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<sup>668</sup> Regression had persisted as Galton would have predicted, but Castle’s rats had not been limited by it.

<sup>669</sup> Castle, “Piebald Rats and Multiple Factors,” 114.

<sup>670</sup> Lashley, Middleton, Stocking

<sup>671</sup> Jennings, “Heredity, Variation and the Results of Selection in the Uniparental Reproduction of *Diffflugia*

to Castle's, reflective of the mostly independent path he took throughout the debate, even serving as a mediator, especially with Pearl, discussed at length below.

Following criticisms of the pure line work from biometricians and from Castle, Jennings searched for an organism that could meet his critics' standards. They had charged that most of the characters pure line workers studied were not "sharply defined and readily determinable," especially size, which was "continually altered during growth" and "greatly modified by environmental agencies." (Keep in mind that over half of Jennings' 1908 publication was dedicated to trying to account for this.) And, as usual, his critics charged he had conducted his experiments for too few generations. Therefore, Jennings sought organisms "multiplying vegetatively [and quickly], with definite structural characters that can be counted and measured, these characters being (1) unchanged by growth; (2) unaffected by the environment during the life of the individual; (3) heritable, yet (4) variable."

He found "this unusual combination of favorable conditions" in *Diffflugia corona*, a shelled amoeba.<sup>672</sup> *D. corona* forms a test of collected sand grains glued together with a "chitinous secretion." The shell had a number of traits unchanged by growth, such as their teeth and spines, as well as dimensional characters that were not modified following development.<sup>673</sup> Jennings thus classified these characters with coat color in birds and mammals, rather than with size. A further advantage of the shell is that it served as a permanent record — after killing the organism, the shell could be stored for later comparisons. Its asexual reproduction recreated an identical test, the original serving as a mold for the new. Thus, its combination of reproductive system, physical characters, and small size were ideal for Jennings' program. Like *Paramecium*, it was not a commodified organism, reflecting Jennings' academic concerns.

Also like *Paramecium*, he collected *Diffflugia* from local ponds and transferred them with capillary pipettes into hollow-ground slides with five to ten drops of water along with washed aquatic plants. While the water was far from standardized, Jennings reported that "an immense amount of time was wasted in attempts to make a culture

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Corona," *Genetics* 1 (1916): 407–534.

<sup>672</sup> Jennings, 410.

<sup>673</sup> Jennings, 413.

medium in the laboratory.” Each slide housed a single organism and Jennings carefully pedigreed every individual using a card catalogue. Between 1911 and 1915, Jennings gathered “four wild collections or ‘populations’” and six “laboratory cultures” (which he also called “populations”). In total, he measured 9,060 individual *Diffflugia*.<sup>674</sup>

By combining biometry with pedigrees, Jennings discovered a large amount of variation among the lineages of wild samples he took from his surrounding environment. In addition, he calculated correlations between some traits, finding that these values varied between populations. (For example, the correlation between parents and offspring in number of teeth was 0.99, but the number of teeth between families varied significantly.) While he considered it possible that individuals tended to “reproduce in some degree the peculiarities of their varying parents” within a homogeneous population (like Castle), he began these experiments still in favor of pure lines, adopting a line similar to Pearl about “securing more” within a population: “in such mixed populations, if we select individuals having a certain character in a higher degree, we shall on the whole obtain specimens having also the other characters in a higher degree.” Jennings appeared to have adopted Pearl’s reasoning that “the effects of selection in populations” was the crux of the debate; his goal was to determine whether selection could improve a stock “within single families.” Such “remain[ed] to be seen,” but until then he maintained his position: “it is indeed extraordinary to see these minute masses of protoplasm reproduce so true to type, yet with such marked diversities between the families. ... It is clear that a population of *Diffflugia* consists of large numbers of different strains, each strain remaining in a high degree true to type.”<sup>675</sup> So far, nothing was different from *Paramecium*. (See Figure 8.)

With *Diffflugia*, Jennings designed a more sophisticated attempt to break a pure line into two. (Note that his original goal was to “bridge the gap,” now it was to “break into two.”) That correlations within a family varied between families led him to wonder if selection could break apart those correlations. That is, “in most families, selection of larger individuals would be on the whole a selection likewise of individuals with more numerous spines and teeth and longer spines. But this would not be the case in all

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<sup>674</sup> Jennings, 415, 418–19.

<sup>675</sup> Jennings, 429, 437, 444.

families.”<sup>676</sup> Thus, could selecting within a pure line “produce from it a set of hereditarily diverse families?”<sup>677</sup> Here we see that while Jennings showed no interest in the practical control of evolution, experimental evolution in itself was an attempt to control evolution.

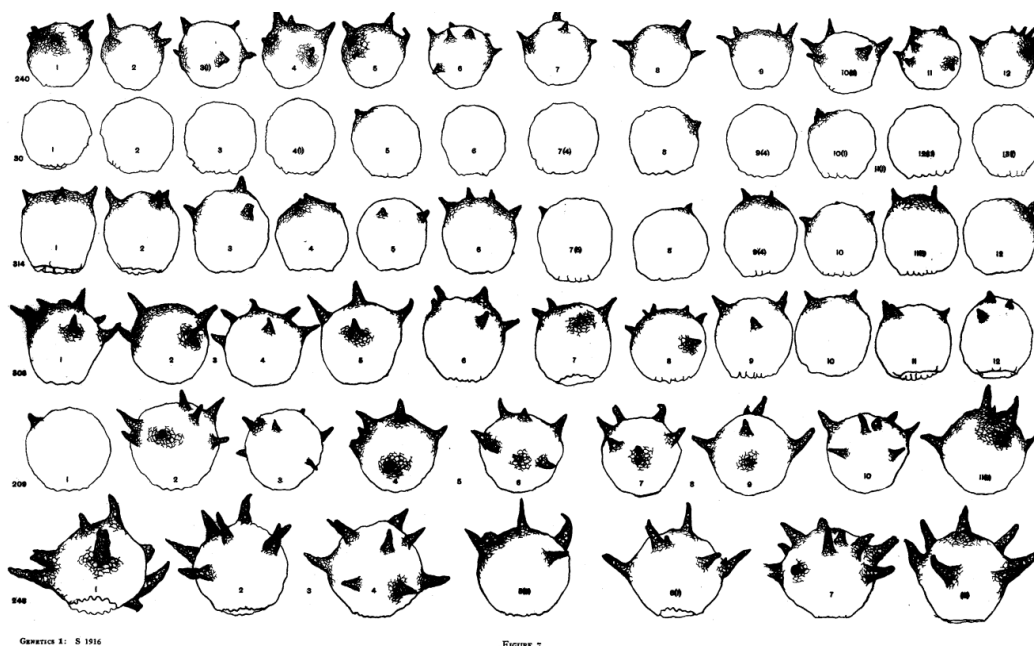


Figure 8: From Jennings, “Heredity, Variation, and the Results of Selection in the Uniparental reproduction of *Diffflugia corona*” (1916), Fig. 7. Each row is a distinct line, and each individual is the immediate progeny of the one to its left. Jennings intended to show that without selection, the lines show distinct and inheritable differences from other lines.

But, contrary to his ‘pure-linist’ expectations, Jennings’ initial study revealed that the evidence pointed to the “inheritance of [new] variations within the single family.” Selecting for increased or reduced number of spines in these two families, Jennings differentiated one family into two “hereditarily diverse” sets. “Selection was effective” also in a family of 1,949 offspring, and importantly, the shifts were gradual, not sudden. Like in Castle’s experiment, one family did show a “sudden noticeable variation inherited

<sup>676</sup> Jennings, 452. That is, similar to his comments in 191x that natural selection would have trouble differentiating inheritable versus non-inheritable variations, selection in this case potentially ran up against family-dependent constraints. [Best way to word that?]

<sup>677</sup> Jennings, 462.

by the descendants — something comparable to a ‘mutation,’” but this was not the trend.

<sup>678</sup> His results continued to contradict his previous work. (See Figure 9.)

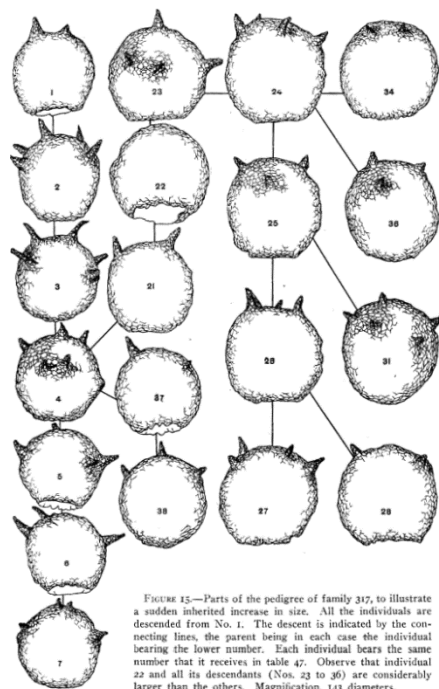


Figure 9: From Jennings, 1916, Figure 15. A pedigree of *Diffflugia* descended from the ancestor at the top-left. Jennings intended to show that unlike his experience with *Paramecium*, *Diffflugia* showed a more marked tendency to vary in size and spine number and length, both by a “sudden noticeable variation” (or “mutation”) as well as small variations (p. 485). Their ubiquity led Jennings to conclude that selection was active and creative.

Jennings set out to account for possible “deceptions,” particularly from growth and

environmental effects. For example, offspring tended to become larger as generations passed. Environmental conditions were also more similar between parent and offspring than between more distant relatives. These tendencies could be removed from consideration “if by selection we can obtain stocks hereditarily diverse for generation after generation...”<sup>679</sup> In a way, this was methodologically accounting for Jennings’ Problem: persistence, and thus inheritance, of a new variation through long experimental time *despite* environmental similarities or differences.

Because the results were “so opposed” to the *Paramecium* work, Jennings replicated the experiment in another family with even more offspring. Over 34 generations, Jennings tracked and measured 4,645 individuals originating from a single individual. In the first six generations, selection had no effect on spine number. Believing

<sup>678</sup> Jennings, 476–85.

<sup>679</sup> Jennings, 467. Jennings also worried that his sample sizes were too small, collecting new wild populations in 1914 from the Johns Hopkins Brickyards to re-examine his contradictory results, producing two families of 496 and 1,050 individuals with distinct correlation figures for shell diameter, number of spines, among others.

his selection was possibly not rigorous enough, Jennings more stringently differentiated the population, paying attention to an individual's offspring (progeny testing) — if an individual with a high number of spines produced offspring with low numbers, or vice versa, Jennings discarded them. Over the next 63 days — six generations — “*selection was effective*. In every period the high parents produce progeny with higher numbers of spines than do the low parents, and the difference is in every case considerable.” When Jennings *ceased* selection for eleven generations, the inherited differences “persisted.” The lines somewhat converged toward the middle, but such regression was to be expected if new variations appeared. Jennings concluded that “it may well be therefore that the inherited racial differences observed in a wild population of *Diffflugia corona* have been similarly produced by differentiation during vegetative reproduction.”<sup>680</sup> He framed his actions as “clearly a breaking up into groups of diverse hereditary size comparable to the diverse families found in a wild population.”<sup>681</sup> Jennings also claimed therefore that his laboratory populations likely showed how evolution in the wild occurred.

Ironically, as Pearl would soon point out to him, Jennings had replicated Pearl's experimental trajectory with hens. Mass selection based on phenotype had failed to increase egg production, but Pearl discovered that if he selected based on progeny, he could quickly sort between pre-existing lines of high- and low-layers. Even though Jennings stated in his conclusion that the discovery of ubiquitous variation in *Diffflugia* was possible partially “by basing selection entirely on congenital characters,” he seems to have not recognized the importance.<sup>682</sup>

Jennings concluded that new variation was relatively common and minute in *Diffflugia*. Considering the contradictory results between *Paramecium* and *Diffflugia*, Jennings lent more weight to the latter precisely because of his attempt to counter his critics through *Diffflugia*'s more reliable characters. He also thought the *Paramecium* experiments may have not lasted long enough, considering *Diffflugia* revealed gradual

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<sup>680</sup> Jennings, 489, 490, 493. Emphasis original.

<sup>681</sup> Jennings, 501–2.

<sup>682</sup> Jennings, 522–523. Selection was not uniformly effective, however, aligning with Castle's caution that selection could not necessarily overcome physiological limits. Jennings could increase the size of *Diffflugia*, but, decreasing size “soon met a complete barrier.” The larger individuals were also weaker, sometimes even producing “offspring” consisting of empty shells. Jennings, 501–2.



changes over thirty generations.<sup>683</sup>

This work placed Jennings outside the Mendelian-mutationist camp and partially in Castle's. He thought the former placed too much emphasis on stability rather than flux. And if variation was more ever-present and renewing, than selection had an important role to play as his own experiment had shown in "breaking" apart pure lines. However, it seems that Jennings did not fully grasp the arguments from East, Shull, and Pearl, but they continued to hash it out.

### Castle's Final Word

In 1917, Castle, Jennings, and Pearl ended the bulk of their experimental work on the nature of variation and "the selection problem." They also hoped to bring the debate itself to a close. While Jennings forged a middle path, Pearl, Castle, and the Drosophilists held fast to their positions.

In "The Role of Selection in Evolution," presented before the Washington Academy of Sciences, Castle interpreted the history of evolutionary science through the context of control, using Darwin and de Vries as representatives of the two poles.<sup>684</sup> Darwin emphasized gradualism, plasticity, accumulation; selection "determine[d]" not only "what classes of variations shall survive," but "what shall be the variable material subjected to selection in the next generation." Therefore, invoking the sliding scale, "*the further evolution of our domestic animals and cultivated plants (and of man himself) is to some extent controllable because we can by selection influence the variability of later generations.*" De Vries, on the other hand, emphasized abruptness, stability, independent mutations (opposed to accumulation), and that selection "exercise[d] no influence on the subsequent variability of the race." Therefore, "*evolution is beyond our control except as we discover and isolate variations.*"<sup>685</sup> Although experimental evolutionists had reached

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<sup>683</sup> There were possible counters, including cytoplasmic inheritance or chromidia, but these were not any more likely than his explanation. In any case, these possibilities were still "material," i.e., "if the nucleus in *Diffugia* may vary gradually, it has the properties attributed to organisms in general by old-fashioned Darwinism," no matter the precise methods of variation and inheritance. Like Castle, Jennings became less concerned with the underlying mechanics. Jennings, 523–25.

<sup>684</sup> Note he continued to consider de Vries his authoritative opponent, rather than his critics, and repeated his misinterpretation of the mutation/fluctuation distinction.

<sup>685</sup> Castle, "The Role of Selection in Evolution," *Journal of the Washington Academy of Sciences* 7 (1917):

consensus with regard to hybridization as a “very potent agency in producing variability,” the question of selection remained as apparently unresolved as when East articulated the problem of evolutionary control in 1903.

The first figures who addressed these questions, Hugo de Vries and Wilhelm Johannsen, left mixed legacies in Castle’s view. De Vries may have conducted selection experiments in maize, buttercups, striped flowers, and four-leaved clovers, but they did not last long enough or sufficiently control for contamination/hybridization to elucidate the interaction between variation and selection. Johannsen was more careful, and Castle now believed the pure line theory was a “safe working hypothesis” for crops in which selection had been shown to be a “waste of time” (due to the rarity of genetic variation in self-fertilizing species). However, Castle rejected the supposed universality of their theories. Pearl’s extensions to sexually reproducing species “met with small success,” thus, no case of a pure line of animals had yet been discovered, although his opponents assumed that the “principle of the pure line” remained applicable.<sup>686</sup> Morgan’s interpretations of the evolutionary dynamics within *Drosophila* were feasible only because he had redefined “mutation” to include “just ordinary heritable variations.”<sup>687</sup> His own work on albinism, an apparently unalterable trait, was ironically the best case, but he considered it the exception to the rule.<sup>688</sup> His opponents’ work therefore remained preliminary at best.

Furthermore, even within pure line theory, selection remained key to improvement. It was required not only to test the validity of a pure line, but to isolate mutations and purify variation within a population. Castle claimed that a “formal adherent of the pure line doctrine” was “pragmatically a selectionist.” Although the theory predicted that selection’s power would cease upon “the attainment of complete homozygosity,” “such a completely stable condition ha[d], ... rarely been

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372–73. Emphasis mine.

<sup>686</sup> Castle, 377–79. “Morgan would undoubtedly admit this since he claims that all heritable variations arise as mutations, but this is simply juggling with names, giving a new meaning to the word mutation in order to justify a sweeping generalization otherwise untenable.” Again, Castle misinterpreted the history.

<sup>687</sup> As I discuss below, Sturtevant and Bridges rejected this interpretation of their work.

<sup>688</sup> Castle also failed to produce guinea pigs that matched the small size of their wild ancestors or the large size of domesticated varieties in South America. He suggested this was due to the changes being “too slow to be observable in the lifetime of one observer” (p. 381).

demonstrated.”<sup>689</sup> The hooded rats and spotted rabbits instead showed that selection’s exhaustion of variation was unlikely, therefore remaining useful.<sup>690</sup>

Ever practical, “...there are very few valued economic characters” which do not blend. Just as Johannsen had never demonstrated size to be Mendelian, Castle pointed to the “weight of carcass, quality of wool, milk production in cattle, egg production in fowls—all these are blending characters which in later generations show either no segregation or imperfect segregation.”<sup>691</sup> (Castle’s claim regarding egg production amounts to a rejection of Pearl’s genetic claims regarding his poultry.) The case was the same for plants — the Illinois corn selection experiment, which East and Shull claimed to demonstrate their theory, should have long since produced a pure line, but instead continued to change. Note, however, that his opponents thought they had addressed this point through multiple factor theory.

Castle asserted that, just as the pure line workers had wished, the debate “has done us great good in dispelling or clarifying the hazy notions which formerly existed as to what natural selection could accomplish.”<sup>692</sup> He accepted the mutation theory’s proposition that selection is “primarily an agency for the elimination of variations, not for their production” and that it acted upon only “variations actually existing.”<sup>693</sup> However,

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<sup>689</sup> Castle, 379–80. “No other method of detecting and utilizing a favorable variation, when it does occur, can be suggested than the very method of methodical and persistent selection against which the pure line advocates direct such vigorous attacks.” Castle, 380.

<sup>690</sup> These contradictions, Castle believed, depended upon geneticists’ “particular choices” of species and characters. He suggested the possibility of “plastic genes” and “fixed genes” to explain the lack of universality, although it seems he never took this notion up seriously. He thought a “perfectly stable gene” to be rare, although the difference could possibly explain Jennings’ contradictory results in *Paramecium* and *Diffugia*.

<sup>691</sup> Castle, “The Role of Selection in Evolution,” 383–84.

<sup>692</sup> Castle also speculated on how his views corresponded with nature for the first time in over a decade, basing his argument in experimental versus evolutionary time. He asked, “If this is true concerning a single character under experimental study for a period of twenty generations, may it not also be true of entire organisms and groups of organisms subjected to keen competition with all other organisms in a struggle for existence which has continued for millions of generations? ... If artificial selection can, in the brief span of a man’s life time, mould a character steadily in a particular direction, why may not natural selection in unlimited time also cause progressive evolution in directions useful to the organism?”<sup>692</sup> This contrasts with East’s comment in Chapter 4 that Lamarckism and to some extent Darwinism may make themselves noticeable and present over a long period of time, but did not seem to be present in experimental time, which was what ultimately mattered.

<sup>693</sup> Castle here is to some extent presciently describing the basis of Darwinism’s “restoration” as described by Stoltzfus and myself: the genetic theory of evolution under the Synthesis accepts the Mendelian-mutationist critiques but claims about the ubiquity of “variations actually existing” means selection was nearly always able to act. See Stoltzfus and Cable, 537–538.

selection, acting as a sliding scale, can “continue and extend variation already initiated by shifting in the direction of selection the center of gravity of variation...”<sup>694</sup> Responding directly to Pearl’s criticism that selectionists misused language regarding causes, Castle wrote:

It is not then a misuse of terms to say that the selection has in this case been the *cause* of further variation in the direction of selection and so an agency in the progressive evolution of a new type.<sup>695</sup>

This was Castle’s final word on the subject until he conceded in 1919. He appears to have been moving toward a synthetic view of evolution (once again) by admitting that one of his opponents’ core arguments – that selection eliminates variation but does not create it – was true. Where his argument now rested was on the nature of causation: new variation was partially determined by where selection left a population after its action. This was close to both sides being in accordance, yet his persistence in denying multiple (and stable) factor theory irked his contemporaries. The rest of this chapter follows Jennings and Pearl hashing out the selection problem based on this debate and the Drosophilist intervention with chromosomal mechanics, before proceeding to Castle’s concession.

### **Jennings and Pearl Grapple with “The Selection Problem”**

Jennings also addressed the Washington Academy of Sciences regarding the implications of his *Diffflugia* work, attempting to resolve the debate “on the occurrence of variations; on the effects of selection; on the method of evolution.”<sup>696</sup> He acknowledged that “the modern experimental study of variation” had demonstrated that genetic

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<sup>694</sup> Castle, 387. On the previous page, he described it this way: “... it is evident that a change in the mean of the character in a particular direction in consequence of selection actually displaces in the direction of selection the center of gravity of variation, so that in a very true sense selection makes possible further variation in that same direction.”

<sup>695</sup> Castle, 386. Emphasis original. He also

<sup>696</sup> H. S. Jennings, “Observed Changes in Hereditary Characters in Relation to Evolution,” *Journal of the Washington Academy of Sciences* 7 (1917): 281–301. Jennings also discussed evolutionary controversies within paleontological work, thinking it confirmed gradualism, but not orthogenesis. He wrote, “we do not observe” orthogenesis in “experimental work; by selection we can move in more than one direction. I do not mean that the possible variations are not limited by the constitution of the varying organism; they certainly are. But there is no indication, so far as I can see, that the variations push in one determinate direction only” (p. 296). Jennings also disputed Bateson’s belief that “evolution has occurred by loss and disintegration” (p. 299).

variations were “permanent diversities; they are static, not dynamic.” From these facts flowed Mendelism and Johannsen’s genotype, concepts to which even Castle should concede.<sup>697</sup> What Castle “must do” is show that this “foundation” is “not final,” “that the diverse existing stocks, while heritably different as the genotypists maintain, may also change and differentiate, in ways not yet detected...”<sup>698</sup>

Jennings characterized the debate as between “genotypic mutationists” and Castle, who alone bore the “full brunt of the attack.”<sup>699</sup> But, Castle had “carried the war into the enemy’s country by predicting that the so-called unit characters in *Drosophila* would be found to be modifiable through selection,” which, according to Jennings, the Drosophilists had since confirmed — at least under Jennings’ interpretation.

Jennings adopted Castle’s (oscillating) disregard for chromosomal mechanics. This fit with his work on *Paramecium* and *Diffugia*, then treated as non-Mendelian organisms. But Jennings also planned “to abandon the ground that Castle would defend, i.e., gametic contamination,” and instead “proceed directly into the territory of the enemy, accept the conditions met there, then see where we come out in relation to the nature of variation, the effects of selection, and the method of evolution.”<sup>700</sup> Although exactly what those “conditions” were remained a matter of dispute, contrary to Jennings’ assertion.

‘Proceeding into enemy territory,’ Jennings reinterpreted the results of the Drosophilists on eye color, emphasizing gradualism over the physical basis of heredity. They had revealed the presence of seven gradations between white and red, in addition to seven modifiers. Jennings considered this a “*pragmatically* continuous series. The extreme selectionist asks only a little more than this.” Although Jennings admitted that the Drosophilists had a different genetic interpretation of eye color’s evolutionary history,

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<sup>697</sup> Jennings, “Observed Changes in Hereditary Characters in Relation to Evolution,” 282–83. Some scientists, such as Jordan, supposed that this sufficiently explained “evolution,” that what was observed was the mere reshuffling of what existed. Instead, Jennings described his now opponents’ views with relative accuracy (especially when compared to Castle): “Organisms forming a multitude of diverse strains with diverse genotypes; the genotype a mosaic of parts that are recombined in Mendelian inheritance; selection a mere process of isolating and recombining what already exists; large changes occurring at rare intervals, through the dropping out of bits of the mosaic, or through their complete chemical transformations; evolution by saltations.” Jennings, 284. Jennings overplayed the Mendelian reliance on saltations.

<sup>698</sup> Jennings, “Observed Changes in Hereditary Characters in Relation to Evolution,” 283.

<sup>699</sup> Jennings, 287.

<sup>700</sup> Jennings, 288. Although Castle himself vacillated between claiming whether or not the underlying chromosomal mechanics mattered.

he took their results as demonstrating the “intermediate conditions” that would allow for a “gradual transition from one extreme to the other,” just as Castle had produced in his rats.<sup>701</sup> Jennings emphasized, “*these modifying factors are themselves alterations in the hereditary constitution.*” Although “there are indeed certain differences in detail,” they were merely over “exactly *where* the changes occur” and this specific dispute — variations in a single factor or reshuffling of modifying factors — “does not touch the fundamental question.”<sup>702</sup> The fundamental question was, for Jennings, the “occurrence of ... minute changes in the hereditary constitution ... [and] the possibility of getting therefrom by selection various grades of a given external characteristic. In this, so far as I can see, there is complete agreement.” To emphasize issues of continuity versus discontinuity when “steps become so minute as to be beyond detection” was “metaphysical” and not “pragmatical.”<sup>703</sup> (Note this is not what his now opponents thought!)<sup>704</sup>

This kind of resolution was possible because both schemes included and allowed for the effectiveness of selection. In Jennings’ view, their differences were over how selection worked and how effective it was. But as Morgan had written, when the theory of natural selection is stated in general terms, “there is nothing in the theory to which anyone is likely to take exception.”<sup>705</sup> But as discussed by Pearl and Jennings below, selection being effective could mean quite different things. (I also showed how East’s

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<sup>701</sup> The Drosophilists held that the gradations themselves in eye color did not come about gradually — red could mutate to white — but, he argued that the eye was already a “complex product of evolution”; mutations breaking the trait now did not necessarily correlate with how the trait was built in the past. Biologists did not know how the eye actually came about genetically. Indeed, Jennings wondered if *Drosophila* showed large changes “perhaps due to the fact that we are witnessing the disintegration of highly developed apparatus in place of its building up.” Jennings, 291, 295–96.

<sup>702</sup> Recall that MacDowell had said selection’s power was not the “ultimate question,” but instead, emphasized the “nature of the changes in the germ plasm.” This should be included in chapter conclusion.

<sup>703</sup> Jennings, “Observed Changes in Hereditary Characters in Relation to Evolution,” 293, 295. He had written along similar lines in his *Diffugia* publication: Whether variation was continuous or discontinuous, he [remarked] that it must be the latter, not within the terms of the debate, but because “in the sense that they involve chemical change,—since all chemical change is discontinuous.” In essence he did not find these distinctions meaningful. He did, interestingly suggest that large mutations in animals and plants may be a result of gradual variation being amplified through development’s cell divisions. Jennings, “Heredity, Variation and the Results of Selection in the Uniparental Reproduction of *Diffugia Corona*,” *Genetics* 1 (1916), 525–26.

<sup>704</sup> Yet oddly the notion that variations could be so minute as to be beyond detection was the opposite of pragmatic; Jennings was unconsciously reasserting his own Problem that the size of fluctuations and mutations could hamper selection’s effectiveness.

<sup>705</sup> Morgan, *A Critique of the Theory of Evolution*, 147.

phrasing of a theory of selection in a seemingly general way was actually quite specific.) Thus Jennings could claim that rather than Castle and the *Drosophilists* representing two oppositional poles,

it appears to me that the work on *Drosophila* is supplying a complete foundation for evolution through selection of minute gradations. ... The objections raised by the mutationists to gradual change through selection are breaking down as a result of the thoroughness of the mutationists' own studies.

He concluded,

evolution according to the typical Darwinian scheme, through the occurrence of many small variations and their guidance by natural selection, is perfectly consistent with what experimental and paleontological studies show us.<sup>706</sup>

However, as the rest of this chapter shows, Pearl, Sturtevant and Bridges, and MacDowell did not accept this formulation of the debate or his conclusions. Whereas Jennings sought resolution through dissolving the poles between Castle and his opponents, their argument was that Jennings had identified the wrong axis. The dispute was not over gradualism or (dis)continuity, but rather over what Jennings tried to mask: selection's interaction with the mechanics of the "hereditary constitution."

That same month Pearl published "The Selection Problem" in the *American Naturalist*. Pearl agreed that the *logic* of natural selection as a progressive factor of evolution was sound but questioned whether selectionists had *experimentally* demonstrated their case. For Pearl,

the question to which we want an answer is not whether natural selection *can* cause evolutionary changes, but rather whether it *does* cause such changes in any significant degree or extent. In other words, we shall prefer the "hard cash" of objective experimental evidence to any logical "promise to pay," however tight and compulsive its reasoning.<sup>707</sup>

Therefore, the biometric work of Bumpus, Crampton, Weldon, and others, whether producing positive or negative results, were insufficient.<sup>708</sup> Pearl's review of the literature

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<sup>706</sup> Jennings, "Observed Changes in Hereditary Characters in Relation to Evolution," 300.

<sup>707</sup> Raymond Pearl, "The Selection Problem," *The American Naturalist* 51 (1917): 68. Emphasis original. Pearl traced the current debate to Weismann's speculative declaration of the Allmacht of natural selection, stated as recently as 1909. Pearl, 65–66.

<sup>708</sup> In this list, Pearl also included di Cesnola, Davenport, Lutz, Harris, Kellogg and Bell, and himself.

led him to believe that even the “experimental and quantitative evidence regarding selective elimination” was “distinctly meager” and the “net result ... not so clear-cut and outstanding as could be wished.” He believed that if a scientist were to visit from another planet and observe the situation, they would conclude

that in some cases natural elimination is certainly in some degree selective, while in other cases it certainly is not; and in the most favorable cases of all the selection is apparently not very rigorous. Grossly teratological abnormalities are eliminated. But the small deviations from type, which in theory ought to furnish the basis of selection, appear upon quantitative study less generally and sharply determinative of survival than might reasonably have been expected theoretically.<sup>709</sup>

Thus, even if Jennings were correct regarding the size and frequency of inheritable variation, it remained uncertain whether selection in nature could detect them. That is, Jennings in 1916 had failed to account for the problem introduced by Jennings in 1908. This may explain why Pearl curiously wrote that many evolutionary changes “come about by relatively large, discontinuous steps,” one of the few instances of a pure line worker declaring so.<sup>710</sup>

According to Pearl, the problem for the theory of natural selection was that it was developed as a “somatic theory.”<sup>711</sup> But any theory of evolution rested on associated theories of variation and inheritance, which had been revised by Mendelism and the “epoch-making researches of Johannsen.” Biologists needed to be “extremely cautious in assuming *a priori* that any particular somatic difference is so inherited.” Another troublesome fact, which MacDowell emphasized (discussed below), was that individuals “possess ... the power of personal, immediate, individual, somatic adaptation to the environment,” negating a “function of any static, single-valued relation between” soma and environment. It would work if selection acted upon the germ cells, but this was rarely the case.<sup>712</sup> Indeed, Pearl noted that when Jennings had worried over whether his

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Pearl, “The Selection Problem,” 69–70. as well as Poulton, Sanders, Reighard?

<sup>709</sup> Pearl, 71. This is somewhat reminiscent of Jennings’ Problem.

<sup>710</sup> Pearl, 74. Keep in mind that he had earlier rejected the notion that mutations were always large. It is also worth noting that most mutationist then did not seek a way out of this dilemma, possibly because their own methods of selection – reducing a population’s variation or heterozygosity – were effective.

<sup>711</sup> Pearl, 72, 74.

<sup>712</sup> Although Pearl had experimentally shown the positive selective effects of alcohol on the germ cells of domestic fowl (but Stockard found it a negative effect in guinea pigs). “Here is real selection making real evolutionary progress.” Pearl, 75.



selections were rigorous enough in *Diffugia*, that he had switched from selecting by an individual's phenotype to the qualities of its offspring. Pearl pointed out to Jennings that this as a change in "the fundamental basis of selection" from somatic to germinal, consistent with his own poultry work.<sup>713</sup> Not only does this point to the pure line workers' acceptance of natural selection, but also their careful distinctions.

Pearl admonished his fellow biologists for their use of statements by practical breeders in support of their own academic theories. Specifically, he charged them for not acknowledging that breeders, unconcerned with or not privy to academic debates, did not use the word "selection" with precision."<sup>714</sup> Furthermore, a systematic study of the origins of cultivated crops revealed selection to be relatively unimportant.<sup>715</sup> In the production of these cultivars, "selection, in the sense of the accumulation of minute favorable variations, has had no part."<sup>716</sup> Instead, the "experience of practical breeders" pointed to "improved conditions of domestication, mutations ..., hybridization ..., and the purification of previously mixed races or varieties by selective sorting."<sup>717</sup> Although Pearl did not note it, this was precisely what East and Shull were doing with maize at the time.

In May 1917, Jennings published an edited version of his address that purportedly ended the "controversy."<sup>718</sup> Jennings wrote,

It is curious to find that their ["mutationists"] studies of *Drosophila* furnished almost all that could be asked by the radical selectionist as to the existence of a single unit character

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<sup>713</sup> Pearl to Jennings (1917/1/15), APS Pearl, Box 15, "Jennings, Herbert Spencer 1914-1918," folder 8. It is also located in Jennings' correspondence papers with Pearl at APS.

<sup>714</sup> Pearl cited an example of a breeder developing a new breed of poultry via a complicated cross who called "the series of matings as ... '*this process of selection*!'" Pearl, "The Selection Problem," 75–76. Emphasis original.

<sup>715</sup> Grape varieties usually resulted from the mere transplantation of "chance seedlings" or some basic hybridization, as was the case for "apples, plums, cherries, strawberries, etc." In the case of the blueberry, a breeder discovered that only an acid soil and a nitrogen-fixing root fungus were required for successful domestication. Pearl's colleague Surface had generated the "Maine 340" oat variety, the most widely grown in the state, by mere isolation. Its nearest competitor originated from an individual discovered on a roadside."

<sup>716</sup> Pearl, "The Selection Problem," 78–80.

<sup>717</sup> Pearl, 81. The history of animal breeding methods was more complicated, but in bantams Pearl found that selection by itself was insufficient.

<sup>718</sup> Jennings, "Modifying Factors and Multiple Allelomorphs in Relation to the Results of Selection," 303.

in in a series of numerous hereditary gradations.<sup>719</sup>

Indeed, “by selective crossbreeding it is possible to bring together into one stock all the modifiers that have been produced in diverse stocks. *Mendelism acts as a tremendous accelerator to the effectiveness of selection.*”<sup>720</sup>

Pearl wrote to Jennings soon thereafter, acknowledging his clarity, and agreed that “the controversy would be at an end, so far at least as I am concerned, ... if the selectionist stopped here, instead of going on to the further, and as it seems to me wholly unwarranted and preposterous assertion to the effect that the *selection is the cause of the alteration in the hereditary constitution.*”<sup>721</sup> While Pearl did not think Jennings believed this, “Castle does & has said it with all the vigor of a fanatic.” Pearl believed that no one disagreed with Jennings’ statement that “selection could accumulate genetic differences if they exist already,” but it was over the *initial cause* of variation where the opposing camps disagreed. Pearl did believe, however, that Jennings held “the key whereby I can work myself out in my own thinking to the right conclusion, as a matter of logic.”<sup>722</sup>

In response, Jennings questioned whether “all your anti-selectionist colleagues agree in admitting all the basic facts for the gradual operation of selection.” (He did not name anyone.) He did agree with Pearl, however, that “it is evident that all that selection can do is to preserve what is already existing; that it cannot originate, or as you put it, ‘initiate variation.’” Indeed, the *Diffflugia* work did not address the origin question because Jennings considered it a settled matter; instead, the work was designed to test “concrete, experimental questions” regarding the size of hereditary variations and whether selection could accumulate these variations in a desired direction. To that end, Jennings was “free to say that to me the answer was not a foregone conclusion and that indeed I was somewhat surprised at the result.”<sup>723</sup> And, contrary to Pearl’s belief, “there was extensive difference of opinion on this matter.” He reiterated that the origin question did not appear to be “the important question” and was instead “non-experimental.” Here,

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<sup>719</sup> Jennings, 303–5.

<sup>720</sup> Jennings, 306. Emphasis mine.

<sup>721</sup> I discuss in the conclusion however that I do not believe Jennings played a particularly “clarifying” role in the debate and was more obfuscatory.

<sup>722</sup> Pearl to Jennings (1917/5/4), APS Pearl, Box 15, “Jennings, Herbert Spencer 1914-1918,” folder 8. Emphasis original.

<sup>723</sup> Note again, however, that mutationists had always emphasized that mutations could be incredibly hard to detect.

Jennings perhaps showed his academic leanings, for the question of the origin of variation was quite a practical matter for many of his colleagues.

The nature of selection remained important to Jennings because he saw no “naturalistic explanation of adaptation save through selection. [Although] I have no leaning toward making selection a general explanation...” Thus, he expounded upon the question, “What can selection conceivably do?” even though he inexplicably considered it “of minor interest.” He sought to clarify the dispute, wondering if Pearl was “in a little danger of having [his] judgement [sic] affected by the spirit of controversy...” In his letter, Jennings differentiated among five plausible effects of selection to which Pearl left marginal notes in response. First, selection can “accumulate” extant hereditary variations. Pearl: “Yes.” Second, “the act of selecting, in a given instance, can have no effect on the variation; cannot ‘initiate,’ cannot produce anything. Here I agree with you completely.” Pearl: “Yes.” Third,

But may not the present selection determine what variation shall or shall not appear? If we find now A, B, and C, and I select A, and kill off B and C, — may not A later produce variations (in its progeny) which B would not have produced, if it had been the one selected? I see no logical difficulty in this; indeed it appears to me probably true. I had always assumed that this was the idea underlying the notion of a ‘dynamic effect’ by selection; or of the production of variation by selection, such expressions are crude and inaccurate things, I supposed they had a reality underlying them.<sup>724</sup>

Pearl noted at this point that “If this is what is meant then why don’t the selectionist say so in his paper?”<sup>725</sup> Indeed, this was rather close to Pearl’s point to Jennings about germinal versus somatic selection. Jennings continued, “If it be true that by the present selection the future variation is determined, in unlimited ages the results might go far. This is what our friend Longley means I take it by his cryptic utterance that selection may affect the course of evolution even though it may not alter the germ plasm.”<sup>726</sup> Pearl: “This is a question of fact. To be answered by *keeping*, not by killing off. *Logically*, it

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<sup>724</sup> This is a somewhat odd statement given that Jennings is the only one to have ever used this phrase, in 1910, as far as I can tell.

<sup>725</sup> For a possible example of what Pearl would have considered the lack of clarity from selectionists, see this quote from earlier from Castle: “*the further evolution of our domestic animals and cultivated plants (and of man himself) is to some extent controllable because we can by selection influence the variability of later generations*” (*Journal of the Washington Academy of Sciences* 7 (1917): 372–73).

<sup>726</sup> This refers to W. H. Longley, “The Selection Problem,” *American Naturalist* 51 (1917): 250–256.

seems probably true. Factually what little evidence there is seems divided [about] equally.”

The fourth and fifth methods of selection were what Jennings thought Castle may possibly support. Fourth, and “rather moonshiny, yet not utterly inconceivable,” was the “possibility that by saving stocks that tend to vary, and killing off those that do not, one can get more and more variation as generations pass?” Pearl: “Yes, but it is in need of experimental trial. ...” Last, is it possible that by “saving stocks that tend to vary in a particular way or direction, and killing off those that vary otherwise, one can get in later generations a more marked tendency to vary *in that direction*? This again seems not utterly inconceivable, though I do not see that there is any evidence that it is true, and to one it seems improbable.”

Although Castle did not participate in this conversation and would not necessarily use their language, it is worth considering where he would have fallen along these distinctions. I suggest that Castle would have agreed with (1) selection accumulates heredity changes, agreed with but had begun to waiver on whether (2) selection initiates variation, asserted most strongly that (3) selection shapes future variation, i.e., the sliding scale, and definitely (5), selection produces further variation in that direction. Whether he would have agreed or disagreed with (4) is unclear, although his brief proposal for the notion of “fixed” and “plastic” genes may matched it. For his part, Jennings figured that Castle meant by “dynamic effect of selection” or “selection causing variation” the last two points, although Jennings did not “hold any brief” for them. Pearl thought these options were “logically” possible, but “Castle’s work does not prove it. Must have individual analysis.” Jennings argued, however, that accepting Point 2 (that selection did not cause initial variation) did not “touch” or logically “annihilate” 4 and 5; instead, they “require to be met explicitly.” Indeed, this is where Castle had ended his argumentation, although not very clearly: he could accept that selection did not create mutations but argued that selection shaped their basis and direction. Furthermore, as clarifying as these distinctions may have been, it also is somewhat of a retreat from the populational perspective that had emerged from East, Pearl, and Shull earlier: Jennings discussed selection in the abstract in the letter, rather than making differences based on the effects of selection in populations.

Jennings thought his ultimately bridgeable differences with Pearl might be due to his “having lived for two or three years in close communion with an organism that persisted in showing slight hereditary variations that could be accumulated, so that by selection marked changes of stock could be brought about. One doesn’t do through such an experience without its leaving an effect!” He proposed a joint paper to Pearl to work out the selection problem, but unfortunately for the historian, Pearl visited Jennings within two weeks of the latter’s reply and a collaborative article never appeared. The American intervention in World War I, in which Pearl worked under Herbert Hoover in the Inter-Allied Scientific Food Commission, may have prevented such work. The next available letter in their correspondence was a little over a year later in which Pearl announced his resignation from the Maine Agricultural Experiment Station to join Jennings at Johns Hopkins as Professor of Biometry and Vital Statistics in the School of Hygiene and Vital Statistics.<sup>727</sup>

### **The Drosophilists Analyze the Physical Basis of Genetic Evolution**

The last major volleys of the debate were launched by the Drosophilists. Although Morgan had commented upon and subscribed to the pure line theory as early as 1903 (and later, the multiple factor theory), his laboratory had mostly engaged from the sidelines, the exception being H. J. Muller’s direct criticism of Castle in 1915. This is not surprising given the laboratory’s preoccupation with the chromosome mapping projects that began in 1912. Starting in 1917, Sturtevant and Bridges, along with Castle’s former student, E. C. MacDowell, used *Drosophila* to counter Castle and Jennings. While Jennings had remarked several times that *Drosophila* supported the arguments of the “radical selectionist,” the Drosophilists themselves advocated a view like East’s and Shull’s based on their practical work with chromosomes.

This section revises Robert Kohler’s depiction of the Morgan lab’s relationship to experimental evolution. According to Kohler, Morgan initially studied *Drosophila* for the purposes of experimental evolution, specifically to test de Vries’ theory of mutation

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<sup>727</sup> Pearl to Jennings (1918/6/1), APS Pearl, Box 15, “Jennings, Herbert Spencer 1914-1918,” folder 8. Double check.

periods. But, he then argues that the dynamics of mutation they discovered “entirely upset any plans for a project in experimental evolution using *Drosophila*.” The flies led Morgan to “gradual[ly] abandon ... this line of work for neo-Mendelian experimental heredity,” a “transition from experimental evolution to modern genetics.”<sup>728</sup> While it is certainly true that experimental evolution was de-prioritized, the lab’s major work, *The Mechanism of Mendelian Heredity* (1915), as well as Morgan’s *A Critique of the Theory of Evolution* (1916), contained extensive commentaries on experimental evolution, including the work of the Jennings’ laboratory. This view further relies upon a partially artificial distinction between experimental evolution and “neo-Mendelian experimental heredity.” But as I have shown so far in this chapter, East, Shull, Pearl, and even Castle and Jennings, integrated Mendelism and selection *through* experimental evolution. Furthermore, Sturtevant and Bridges directly engaged Castle and Jennings with original work in experimental evolution by redeploying their chromosome mapping techniques in its service.

Beyond criticizing his former mentor for misinterpreting his results as contrary to pure lines, factor constancy, and multiple factors, E. C. MacDowell at the Station for Experimental Evolution took up *Drosophila* to provide a new positive contribution in the late stages of these debates. MacDowell took on the issue of “genetic indeterminism.” Whereas Pearl had asked if selection alters a population or a character, MacDowell considered “the crux of the selection problem [to be] whether abnormal parents have abnormal children. Specifically, it is, do parents with higher bristle grades produce children with higher bristle grades?”<sup>729</sup> Thus, MacDowell addressed Pearl’s charge against Castle that his theory consisted of “genetic indeterminism.”

MacDowell conducted pure line and selection experiments on mutations for more or fewer bristles, reminiscent of Castle’s hooded rats, yet arrived at opposite conclusions. MacDowell was able to make use of the experimental virtues of the fly: he propagated

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<sup>728</sup> Robert E. Kohler, *Lords of the Fly: Drosophila Genetics and the Experimental Life* (Chicago: University of Chicago Press, 1994), 43–45.

<sup>729</sup> MacDowell, “Bristle Inheritance in *Drosophila*. II. Selection,” *Journal of Experimental Zoology* 23 (1917), 119. MacDowell, 119. This is Jennings’ fifth form of selection, Castle’s sliding scale.

flies for 49 generations, counting over 100,000, easily surpassing Castle's 33,000 rats.<sup>730</sup> Each generation was the progeny of two parents, a bottleneck that allowed rigorous inbreeding without necessarily injuring the stock's vigor. In the early stages, selection rapidly increased, but later ceased to change the mean number of bristles, replicating the varying rate of change he derived from Castle's data, and pointing to selection as an isolating mechanism.<sup>731</sup> He detected strong, but impermanent and random fluctuations due to environmental changes or methodological shortcuts.<sup>732</sup> MacDowell also collected the data for extreme variations, finding that the lower limit never increased and the highest point occurred early in the experiment and was not inherited.<sup>733</sup> He also found that "high parental averages are not accompanied by high filial averages," and rather the means were transmitted, i.e., somatic appearance and genetic variation were not 1:1.<sup>734</sup> The flies demonstrated what MacDowell saw in the rats, and conformed with Pearl's Mendelian-mutationist argument. In contrast, Castle's theories of a single varying factor, potency, and gametic contamination could not account for the failure of reverse selection or the restoration of selection's power after crossing a selected line with normal flies.<sup>735</sup>

However, the fluctuations MacDowell presented a problem along the lines of "Jennings' Problem," the possibility that fluctuations from environmental effects mask genetic variation from selection's view. Initially, selection was capable of sorting between heterozygous stocks. But the variation that remained in the genetically homozygous stocks MacDowell concluded was mostly due to age and environmental action, the latter enough so that "the number of extra bristles appearing can be controlled to a certain extent;" not by selection, but through the environmental manipulation of nutrition, moisture, and temperature.<sup>736</sup> This was shown by contemporary experimental lines

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<sup>730</sup> This paper does not provide sample sizes, but MacDowell mentions this number in "The Bearing of Selection Experiments with *Drosophila* upon the Frequency of Germinal Changes," *PNAS* 3 (1917): 292.

<sup>731</sup> MacDowell, "Bristle Inheritance in *Drosophila*. II. Selection, 124–25.

<sup>732</sup> MacDowell, pressed for time during some generations, could not count all the flies; flies that emerge earlier tend to have more bristles, skewing the data. Generations 32 to 49 were raised in constant temperature rooms to eliminate environmental confounding (p. 113).

<sup>733</sup> MacDowell, "Bristle Inheritance in *Drosophila*. II. Selection," 109–16.

<sup>734</sup> MacDowell, 122–23.

<sup>735</sup> To account for the restoration of selection's power following a cross with normal flies, "contamination theory" entailed that the "allelomorphic mates" must "fuse" and "then that this fusion weakens the power of that factor for forming extra bristles," but in some cases must not be weakened at all.

<sup>736</sup> MacDowell, "Bristle Inheritance in *Drosophila*. II. Selection," 139.

exhibiting parallel changes over time. MacDowell thought this conclusion, that the environment could “overpower” genetic differences, was worthy of more attention. It may allow for some human control over biological growth, but it produced methodological problems for experimental evolution: MacDowell suggested that Castle “ignore[d] the scope of the influence of environment.” Instead,

... there is very little support for the supposition that the soma mirrors the germ plasm in all cases except when obvious environmental relations are found. It seems hardly possible that one can look forward to ever establishing firmly an exact relationship between soma and germ plasm, at least in bi-sexual multicellular animals.<sup>737</sup>

However, MacDowell was cautious to not extrapolate too far from this experiment. One could claim that MacDowell’s experiment could not detect small germinal changes akin to *Diffugia*’s. But MacDowell in turn claimed that the opposing camp had not fully controlled for environmental effects. And when considering practical conditions, a breeder could never hope for the standardized environment that would reveal such minute genetic variation. Thus, MacDowell adopted a version of Jennings’ Problem:

The claim [that undetectable variation is occurring] may be made, but it will give neither the breeder, nor natural selection any opportunity to make progress. It appears that instead of offering a fatal objection to the work here reported, the evident environmental factor serves well to emphasize the utter futility of attempting to deal in theory or fact with supposed germinal phenomena that can never be demonstrated or utilized.<sup>738</sup>

To whom this assertion was directed is unclear, but it seems likely that he was challenging Jennings’ claim for the universality of new variation’s ubiquity. He concluded “no change that could have either evolutionary or practical significance has occurred in these units [determining bristle number] during the 50 generations of the experiment.”<sup>739</sup> To some degree, MacDowell foreshadowed Castle’s own pessimistic conclusion in 1919.

The *Drosophilists* Alfred Sturtevant and Calvin Bridges hammered at Castle’s

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<sup>737</sup> MacDowell, 140.

<sup>738</sup> MacDowell, “The Bearing of Selection Experiments with *Drosophila* upon the Frequency of Germinal Changes,” 296.

<sup>739</sup> MacDowell, 297. In 1920, MacDowell calculated new correlation coefficients and confirmed the conclusions he presented in this paper. Edwin Carleton MacDowell, “Bristle Inheritance in *Drosophila*. III. Correlation,” *Journal of Experimental Zoology* 30 (1920): 419–460.



theories of gametic contamination and selection's creativity. Having developed the chromosomal theory of heredity using linkage mapping techniques, Sturtevant and Bridges now deployed it to address evolutionary questions, without which "any claim that factors can themselves be changed can have no finality."<sup>740</sup> In contrast to how Castle and Jennings hedged on questions of the mechanics undergirding evolutionary change, they were able to demonstrate the existence of modifying factors and their implications for evolution. This is an important historiographical point: the Morgan lab at this time, and especially his students, are usually portrayed as just (physical) geneticists, but they also saw their work as part of a larger science of evolution.

Published by CIW, "An Analysis of the Effects of Selection" was the *Drosophilist* answer to Castle's guinea pigs. Focusing on "variability in bristle number" in the Mendelian mutant *Dichaet* ("two-bristled"), Sturtevant, starting from a range of zero to seven bristles, selected in the plus and minus directions, crossed them, tested for the presence of modifying factors, and argued against contamination. He concluded, unsurprisingly, that "selection is usually effective only in isolating genetic differences already present; and that genes are relatively stable, not being contaminated in heterozygotes, and mutating only very rarely."<sup>741</sup> MacDowell had also conducted selection experiments with bristle number, but his flies did not vary to the degree that *Dichaet* did, possibly providing material for selection.<sup>742</sup>

Sturtevant reduced the selection problem and the method of his experiment to the following formula: if Castle was right, then selection should be as effective within inbred stocks as any other, but if his opponents were right, then the rate of change should slow down quickly but regain speed when crossed (due to more modifying factors to sort between).<sup>743</sup> There were four experimental lines: inbred plus and minus and crossbred plus and minus, carried out for up to fourteen generations with a total of 3,504 flies,

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<sup>740</sup> Finding a mutation for shorter wings (truncate), the laboratory bred the culture for shorter wings for three years. They were then able to locate at least three modifying factors and even isolate and recombine them. Morgan, *A Critique of the Theory of Evolution* (Princeton: Princeton University Press, 1916), 166-170.

<sup>741</sup> Sturtevant, *An Analysis of the Effects of Selection* (Washington, D.C.: CIW, vol. 264, 1918), 3.

<sup>742</sup> Sturtevant, 4-5. Like MacDowell, Sturtevant checked for environmental effects, finding some significant differences between "broods" with identical pedigrees raised in separate bottles. Because they were inbred for four generations, he considered differences in modifying factors, such as genetic differences in rates of crossing-over, unlikely. Sturtevant, 6-7.

<sup>743</sup> Sturtevant, 8-9.

finding that the mean bristle number did not significantly change. Reverse selection had no effect. One line did respond to minus and reverse selection, providing “perhaps the clearest evidence of the effectiveness of selection that we have yet observed.”<sup>744</sup> Yet Sturtevant maintained that the wealth of evidence pointed towards the Drosophilists’ theory of multiple modifying factors.

In a complicated series of crosses, Sturtevant used linkage mapping to *find* the modifiers. He located modifiers on the second chromosome in addition to one or two on the third. He also identified mutations and determined whether they were allelomorphs or modifying factors, “a striking illustration of the danger of arguments as to the identity of characters based on similarity of appearance.”<sup>745</sup>

According to Sturtevant, *Dichæte* flies were a perfect test of Castle’s theory of gametic contamination. Because *Dichæte* was lethal when homozygous, making *Dichæte* flies necessarily heterozygous, half of their offspring were wildtype homozygous flies. If contamination were true, a stock kept for more than forty generations *should* contain wildtype flies with fewer bristles than usual given they were borne of heterozygous parents in which the gametes united and perhaps blended. However, Sturtevant claimed that “there is no evidence that any progressive change has occurred...” In the selected stocks, normal flies occasionally had fewer bristles in the minus series and more bristles in the plus series (with only one exception among 477 flies), not unexpected if modifiers were accumulating.<sup>746</sup> The experimental evidence of more than forty generations, combined with Sturtevant’s detailed dismissal of Castle’s list of cases of gametic contamination, contradicted Castle’s entire theory.<sup>747</sup>

Sturtevant provided his analysis of the “selection problem.” Whether selection was responsible for *de novo* “germinal differences” Sturtevant considered “incomprehensible” and without evidence.<sup>748</sup> Citing MacDowell, he suggested that the

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<sup>744</sup> Sturtevant, 10–19, 22–23.

<sup>745</sup> Sturtevant, 23–28, 32–34.

<sup>746</sup> Sturtevant, 34–35.

<sup>747</sup> According to Sturtevant, the known cases of contamination were consistent with multiple factors, remained untested, or were based on unreliable data. Combined with the evidence *against* contamination, provided by Sturtevant and Muller, and how Castle resorted to “non-genetic factors,” it was Castle’s theory that was now superfluous. Sturtevant, *An Analysis of the Effects of Selection*, 39–46.

<sup>748</sup> Bridges’ take on this question was that “there is not one iota of evidence to show that either the rate or the direction of the mutation processes” are “altered by such selection.” However, in large populations or “when mutation in the direction of selection occurs, there should be a jump in the speed of progression.”

evidence in favor of such a scheme was likely the result of the scientist “examining his animals or plants for that character with unusual care,” an experimental artifact. Instead, mutations could occur during an experiment independently of selection, but because these were relatively rare, selection instead mostly relied upon extant variation.<sup>749</sup> This was especially the case when one considered that most populations were not inbred, hence “likely to be heterozygous for factors influencing many characters,” including modifiers.<sup>750</sup> Sturtevant also suggested that the linkage mapping work logically entailed that a majority of mutations would occur within the more frequent modifiers than in the main factors. As Bridges pointed out, Castle’s theory required “repeated mutation in a single locus,” which was “theoretically possible,” but unlikely. Any genetics-based experimental evolution needed to demonstrate that these variations were not already present in the stock.

Bridges’ response to Jennings’ use of *Drosophila* eye color the following year tackled Castle’s sliding scale theory. Whereas Jennings claimed that Bridges had shown eye color mutations to fall along a unidimensional spectrum, the historical “origin” of “these modifiers were entirely independent of one another.” Because of their careful record keeping, Bridges could show their independent origins: *Cream a* appeared on July 15, 1913, and *Cream c* appeared on July 21, 1916. Bridges demonstrated that the order of their occurrence bears only a random relationship to this spectrum, a “purely artificial and descriptive scale.” Therefore, Castle’s sliding scale theory did not apply: the genetics showed there was no scale to slide along. Rather, selection was able to act upon a “multiple heterozygous stock” made of a “combination of several ... simple modifiers.” Bridges asserted, contrary to Jennings, that Castle’s hypothesis was “parallel,” but *not identical*.<sup>751</sup>

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Bridges, “Specific Modifiers of Eosin Eye Color in *Drosophila Melanogaster*,” *Journal of Experimental Zoology* 28 (1919): 380.

<sup>749</sup> Sturtevant thought this was the explanation for Castle’s “mutants” and wondered why Castle considered it a special case, rather than the norm for all variation.

<sup>750</sup> Later in the paper, Sturtevant addressed the need for published pedigrees to determine whether Castle’s inbreeding was sufficient to eliminate initial heterozygosity. He cited examples from thoroughbred horses that demonstrated the need. Sturtevant, 47–48.

<sup>751</sup> Bridges, “Specific Modifiers of Eosin Eye Color in *Drosophila Melanogaster*,” 371, 381, 338, 378. Bridges described how evolution would work in this way: “The first result of selection in such a heterogeneous stock in the direction of lighter forms would be to pick out individuals homozygous for one or more of the modifiers and probably heterozygous for others. These different individuals of course would

Bridges also addressed the question of variation size and the definition of mutation. Although Jennings and Castle claimed that the *Drosophilists* had redefined the word to suit their theory, Bridges countered that this broader interpretation, which did not originate with them, was clarifying. Bridges wrote,

In our opinion, the attempted distinctions between ‘saltations,’ ‘mutations,’ and ‘variations of slight degree’ have led rather to confusion of thought than to clearer thinking. To us these are all a single class, ‘mutations,’ and the term carries no restrictions of degree, covering the most extreme as well as the slightest detectable inherited variation.<sup>752</sup>

Perhaps to the *Drosophilists*’ own detriment, Bridges noted they tended to focus on visible mutations. They were aware of the trade-offs of their work: slight mutations were probably more important biologically and evolutionarily, but extreme mutations were experimentally tractable. This dialectical argument, that qualitatively these quantities were essentially the same yet differed in experimental tractability, is what allowed them to experimentally counter Castle.

Sturtevant concluded with a summary of the theoretical results of their work:

That many characters may be influenced by more than one pair of genes has long been recognized, and this is the essence of the multiple-factor view. That genes exist which require the action of other genes before they produce visible effects has also been long known. Furthermore, that there are genes which produce very slight visible effects is now another commonplace. Given these three facts, and the hypothesis (which is supported by much specific evidence) that most races are heterozygous for a number of such genes is all that is required to complete the conception that is held by most adherents of the view that multiple factors or modifying genes are responsible for the results of selection. ... Factors do change, and more than two forms are possible for certain loci; but there is no known method of inducing such changes, and they are ordinarily quite rare and definite.<sup>753</sup>

Therefore, in the views of Sturtevant and Bridges, the mutationist and pure line

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not necessarily be homozygous for the same factors, and therefore the population might still remain heterogeneous for these factors. Continued selection would result in a greater and greater degree of homozygosity and homogeneity and a consequent slowing down of the speed of the progression of the population in the direction of selection. The grade of the form reached when the population is homozygous and homogeneous would depend on the number and character of the particular modifiers in the initial population” (p. 378).

<sup>752</sup> Bridges, 382.

<sup>753</sup> Sturtevant, 51.

theories of evolution and selection proposed by their laboratory as well as by East and Shull was consistent with a Mendelism upon which they had also elaborated and made physical. Furthermore, this shows that the Drosophilists had evolution in mind as they conducted their genetics work and made a serious contribution to its development through this debate.<sup>754</sup> Sturtevant's and Bridges' independent and late intervention in the debate shows how there was a conceptually distinct and coherent theory of evolution that united most of the experimental evolutionists despite their lack of central and united program (as seen in the Synthesis).

### Castle's Concession and the Limits to Control

In 1919, Castle conceded. His former student, Sewall Wright, had suggested a “crucial experiment.” Wright, who had long accepted the evolutionary and genetic views of East, proposed an experiment that could determine whether the hooded factor was modified by accessory factors. Castle crossed plus and minus lines with a third wildtype race. He then extracted the hooded character as a recessive in the F<sub>2</sub> generation. As he repeated these crosses, they rapidly converged as modifying factors were removed. He concluded “that three or at most four crosses with a wild race suffice to obliterate all the racial differences which had been induced by ten generations of selection in the case of the plus race and sixteen generations in the case of the minus race.” Castle pointed out that Phillips and he had offered this scenario as a possibility in their 1914 publication but had considered the evidence insufficient. But with this crucial experiment in addition to the Drosophilists' linkage techniques showing the presence of modifiers, the opposing view was “greatly strengthened.”<sup>755</sup> While Castle apologized for his “own obtuseness,” he defended the usefulness of his adversarial role: he “recall[ed] with satisfaction how much clearer the rôle of selection now stands revealed than it did when these experiments

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<sup>754</sup> Oddly, though, Sturtevant's selection experiment did not leave a legacy within the Morgan lab; for example, Dobzhansky, despite being a close collaborator of Sturtevant in the 1930s, never mentioned it. I suggest this is due to their physical proximity (i.e., lack of correspondence) and that the debate's conclusion meant that later scientists would not cite individual articles and instead accept the results as general knowledge.

<sup>755</sup> W. E. Castle, “Piebald Rats and Selection, A Correction,” *The American Naturalist* 53 (1919): 373.

were begun...”<sup>756</sup> His work also showed that even if he misunderstood the genetic mechanics of his experimental systems, selection was arguably creative and powerful, influencing Fisher, among others.<sup>757</sup>

Castle did not fully adopt his opponents’ position, finding a way to keep the creativity of selection. He agreed with Jennings that mutations were more common than usually thought, in both pure lines and cross-fertilizing species, thus allowing for selection to operate. This was shown especially by the research on maize by Emerson and Hayes. It was just that “modifying factors rather than repeated mutation seems to be the explanation...”<sup>758</sup> Castle also argued that when he had begun his work, “he was treated as a traitor to Mendelism who saw any utility in selection or advocated its use as a means of improving the inherited characters of animals or plants.”<sup>759</sup> Now, “that selection ... is an effective agency in producing racial changes is not questioned to-day...”

Castle hoped that this was not the end of the story for experimental evolution. Although there was no evidence in its favor, he wondered “whether the direction of genetic variation is controllable, other than by manipulation of modifying genes or the discovery of multiple allelomorphs...” Whether or not a breeder could “produce variability of a genetic character” remained to be determined. But with pessimism, Castle concluded his now seventeen-year-old mission to control with evolution with the remark: “we certainly at present have to follow nature’s lead rather than to lead nature, as regards the course of evolutionary change.”

## Conclusion

In 1910 Shull declared that it was “the era of experimental evolution.”<sup>760</sup> Yet few if any historians have described this time period as such. What these two chapters have

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<sup>756</sup> Castle, 374.

<sup>757</sup> Gayon, *Darwinism’s Struggle for Survival*, 314.

<sup>758</sup> Castle, 375. In a footnote, Castle complained that Sturtevant had misrepresented his definition of contamination. Castle claimed that he only ever applied contamination to the visible character, not the genetic factor itself. Thus, he considered the addition or subtraction of modifying factors to be a form of contamination. Either Castle is misrepresenting the history (as he repeatedly did with regard to mutation size) or never clarified what he meant.

<sup>759</sup> Castle, 374.

<sup>760</sup> George Shull, “Heredity as an Exact Science,” *Botanical Gazette*, 1910, 226.

done is help establish that Shull was correct. While historians would see much of the content as genetics, the scientists saw it as the experimental study of evolution as a *process* to be controlled. Furthermore, Shull and East, especially, initially took more influence from Hugo de Vries, Wilhelm Johannsen, their breeder contemporaries, and even Darwin, than they did William Bateson and Gregor Mendel. That Castle did initially take inspiration from Bateson and Mendel, yet became one of Mendelism's main antagonists demonstrates that viewing this era as broader than just Mendelism and genetics is essential to understand what happened. Additionally, Jennings worked entirely without Mendelian theory. I suggest then that Stoltzfus and I were correct to call this loosely agreed-upon theory that emerged from their work as Mendelian-*mutationism*.<sup>761</sup> And, I argue that experimental evolution should become a more prominent category in the historical analysis of biology in the early twentieth century: it describes their motives and approach to process, but without tying all scientists into a theory (Mendelism, genetics, etc.) with which they did not always agree.

The arguably most intensive attempts to scientifically *control* evolution led to a more precise understanding of the genetic process of evolution by 1920. Biologists now saw selection as acting upon a population's genetic makeup, increasing or reducing inheritable variation or its heterozygosity and homozygosity. They also had a better understanding of inbreeding and hybridization (although the notion of "hybrid vigor," or later, "heterosis," still required explanation). Mutations versus fluctuations was a key distinction to make with major implications to work out, even if in retrospect it seems rather banal. I have also pointed out throughout the chapter that these biologists were in the process of making the transition to "population thinking." Ernst Mayr, who coined the distinction between typological/essentialist and population thinking, argued somewhat similarly, when he briefly notes that contrary to de Vries and Johannsen, "other geneticists who had entered genetics from natural history or from animal or plant breeding, like Nilsson-Ehle in Sweden, East, Jones, Jennings, Castle, and Payne in the United States ... made findings which showed that there is no conflict between the genetic evidence and either natural selection, gradualness of evolution, or population

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<sup>761</sup> Arlin Stoltzfus and Kele Cable, "Mendelian-Mutationism: The Forgotten Evolutionary Synthesis," *Journal of the History of Biology* 47 (2014): 501–46.

thinking.” Yet, as I have shown in Chapters 2, 4, and 5, their theory of evolution emerged from de Vries and Johannsen: Mayr labeled their theories as “antiselectionist” and “saltational,” but I argue that this is too one-sided and ignores that a rejection of Darwinian selection does not make one “anti-selectionist.”<sup>762</sup> Mayr’s static dichotomy allows no space for latency, emergence, and transition that is the hallmark of this period in the history of evolution. Rather, de Vries, Johannsen, East, Shull, Castle, Jennings, Pearl, the Morgan lab, among others, all contributed to what Jean Gayon called a “kinetic” theory of selection within a population that was then mathematized by the theoretical population geneticists, Wright, Fisher, and Haldane.<sup>763</sup>

Jennings himself offered his own version of events as they occurred which is worth remarking upon. In one intriguing quotation, Jennings remarked:

it appears to me that the work on *Drosophila* is supplying a complete foundation for evolution through selection of minute gradations. ... The objections raised by the mutationists to gradual change through selection are breaking down as a result of the thoroughness of the mutationists’ own studies.<sup>764</sup>

I argue that this is somewhat misunderstanding what happened. Both Jennings and Castle attacked strawmen, emphasizing that the mutationists argued for large mutations whereas Darwinians argued for small variations, whereas the mutationists almost always emphasized themselves that mutations could be of any size. The hailing of the *Drosophila* work as correcting this purported mistake is common, but incorrect. Where Jennings is correct, though, and I have never been sure if he was being genuine or sarcastic in this passage, is that the mutationists were indeed responsible for putting forward a “complete foundation for evolution through selection of minute gradations”: it is just that they never rejected either selection or minute gradations, but changed what both terms meant! That Jennings did not appreciate this fully was shown by his analysis of *Drosophila* eye color which Bridges countered.

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<sup>762</sup> Ernst Mayr, *The Growth of Biological Thought* (Cambridge, Mass.: Belknap Press, 1982), 550.

<sup>763</sup> Jean Gayon, *Darwinism’s Struggle for Survival: Heredity and the Hypothesis of Selection* (Cambridge: Cambridge University Press, 1998), 308-314.

<sup>764</sup> Jennings, “Observed Changes in Hereditary Characters in Relation to Evolution,” 300. He made a similar remark in his other 1917 paper: “It is curious to find that their [“mutationists”] studies of *Drosophila* furnished almost all that could be asked by the radical selectionist as to the existence of a single unit character in in a series of numerous hereditary gradations.” From “Modifying Factors and Multiple Allelomorphs in Relation to the Results of Selection,” 303-305.



Yet, ironically, through control, these scientists had also encountered limitations.<sup>765</sup> As Castle concluded, they had “to follow nature’s lead rather than to lead nature, as regards the course of evolutionary change.” Castle had for 15 years pushed for selection’s creativity – that it not only shaped a population’s genetic composition, but that it itself produced the genetic changes necessary for it to operate. Yet, Shull and East would probably not recognize Castle’s pessimistic conclusion. Sure, mutations were independent and random with respect to selection, but selection, combined with inbreeding and hybridization, remained powerful tools for controlling evolution. A particularly intriguing practical application developed by East and Shull (with Donald Jones and Henry Wallace) was hybrid corn using inbred lines, which emerged from this science of experimental evolution, yet bears little resemblance to how evolution works in the wild; an artificial yet dialectical pole to Mendelian-mutationism.<sup>766</sup>

As messy and complicated as this debate within experimental evolution was, this was a *serious attempt to understand and control evolution*. This was true even if not all the biologists involved, such as Jennings and Sturtevant, articulated their own motivations as such – since other participants integrated their work into their mission to control. The debate also cohered through the Station for Experimental Evolution and

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<sup>765</sup> As Friedrich Engels remarked on this sort of contradiction, “Thus at every step we are reminded that we by no means rule over nature like a conqueror over a foreign people, like someone standing outside nature - but that we, with flesh, blood, and brain, belong to nature, and exist in its midst, and that all our mastery of it consists in the fact that we have the advantage over all other beings of being able to know and correctly apply its laws.” From “The Part Played by Labour in the Transition from Ape to Man” (1876) in *Dialectics of Nature*, indexed at <https://www.marxists.org/archive/marx/works/1876/part-played-labour/index.htm>.

<sup>766</sup> There has been considerable debate over the impact of genetics on agriculture. The consensus appears to be that genetics may not have contributed *new* breeding methods but helped explain and rationalize the methods that did exist. I touch on this question in the Conclusion. For more on the science behind the development of hybrid corn, see Deborah Fitzgerald, *The Business of Breeding: Hybrid Corn in Illinois, 1890-1920* (Ithaca: Cornell University Press, 1990). Barbara Kimmelman and Diane Paul argue that the success of hybrid corn was due not only to experimental evolution but American political economy. East and Jones in 1919 acknowledged that selection in maize could produce better strains than the hybrid method; however, such strains would be propagatable by farmers, whereas hybrid corn was patentable by the seed companies (“Mendel in America: Theory and Practice, 1900-1917,” in *The Development of American Biology*, eds. Keith R. Benson, Jane Maienschein, and Ronald Rainger, 263–83 (New Brunswick: Rutgers University Press, 1988)). But as Roll-Hansen points out, this alternative but unused method was borne from the same science as double hybrid corn (“Theory and Practice: The Impact of Mendelism on Agriculture,” *Comptes Rendus de l’Académie Des Sciences-Series III-Sciences de La Vie* 323 (2000), 1114). Thus, double hybrid corn as one of experimental evolution’s most important impacts is not negated but was one of several options that emerged from the science of experimental evolution. For Pearl’s perspective on his work’s applicability to agriculture, see Kathy J. Cooke, “From Science to Practice, or Practice to Science? Chickens and Eggs in Raymond Pearl’s Agricultural Breeding Research, 1907-1916,” *Isis* 88 (1997): 62-86.

CIW, which funded (and published) the work of Shull, Castle, and the Morgan laboratory, alongside the Maine, Illinois, and Connecticut Agricultural Experiment Stations. My dissertation treats their work seriously as theoretically and practically important, even though like all sciences, it had limitations and blind spots.

Castle articulated the limits and power of experimental evolution, or “experimental breeding” as he called it in “The Role of Selection in Evolution.” He did not think the method was superior to paleontology, biogeography, and other field studies. What made it unique was that “the experimental breeder can study a few successive generations with an intensiveness that is possible by no other method.” Yet, “his glimpses of evolution at work are momentary.” In a sense, the experimental evolutionist could see microevolution, but not the macroevolution of the paleontological record; he could “witness the production of new *sorts* but it is doubtful whether any man has witnessed the contemporary production of a new *species*.” However, pointing once again to control, Castle concluded that the breeder “deal[s] with the *actual material* concerned in organic evolution. He can *see* and *handle* it and observe it change under his hands.”<sup>767</sup> Experimentation held the potential to make evolution visible, controllable, and useful, even if not quite yet.

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<sup>767</sup> Castle. “The Role of Selection in Evolution,” *Journal of the Washington Academy of Sciences* 7 (1917): 374.

## Dissertation Conclusion

I began this dissertation on the history of experimental evolution not with Charles Darwin, but with the late eighteenth-century livestock breeder, Robert Bakewell. As Darwin himself argued, humans had gradually exercised more control over the future direction of their livestock and crops, first unconsciously, but with Bakewell and his contemporaries, more systematically. Systematic breeding, which involves artificial selection, inbreeding and outcrossing, hybridizing, progeny testing, and the creative foresight of the breeder, emerged alongside British capitalism, enclosure, and market formations. But its gradual emergence from unconscious human interaction with nature allowed Darwin to make a leap from artifice back to nature: artificial selection was a special type of natural selection. While Darwin's influence from breeders is well-known, considering it forms the bulk of the *Origin's* first chapter, they have been overshadowed by Thomas Malthus. Both breeders and Malthus were capitalist influences on evolutionary thought, but importantly, breeders, through their practice and intervention upon the world, demonstrated inheritable variation and the power of selection. It was what Darwin called "an experiment on a gigantic scale." Breeding was arguably impactful enough that Darwin's theory of natural selection is, in large part, a theory of pigeon breeding. Thus, I argued that evolutionary science itself is rooted in experiment, and that it emerged from practice; experimental evolution precedes, in some sense, evolutionary thought. For Darwin, evolution was already visible, controllable, and useful, despite his own personal disinclination to develop the science in that direction.

Gregor Mendel, I argued, is rather similar. Moravia was another major European breeding center that had established societies and journals to develop breeding methods and knowledge. This culture in turn influenced Mendel. While he is not typically considered an *evolutionary theorist*, the integration coming decades later, I argued he worked within a tradition of *experimental evolution*. His famous paper, "Experiments on Plant Hybrids," followed his predecessors' work on what he called the "*transformation of one species into another through artificial fertilisation*." Despite working in a garden with *Pisum*, Mendel saw no reason a plant would obey different natural laws under his

tight control than in nature. He shared a common regard with Darwin for the use of artificial conditions to understand the wider world.

I argue, therefore, that much like how the steam engine preceded thermodynamics, the practical methods of systematic breeding preceded the theories of natural selection and alternative inheritance. When phrased this way, it seems obvious, but it therefore means that *experimental evolution is at the heart of evolutionary science*. Evolution was being controlled and used before it was scientifically understood; it being controlled and used was *how* it became understood.

That a more conscious and direct experimental evolution was available at the time, but not taken up, is demonstrated by the curious case of Reverend Dallinger's long-term selection experiment. The work is frequently noted by today's experimental evolutionists yet has not been mentioned by a single historian of biology. (The sole historian to discuss his work is J. W. Haas, Jr., a scholar of science and religion.) It had little to no influence on later developments – Davenport did not even mention him in his historical notes! – but did show experimental evolution's promises and limitations. From the sophisticated (and vulnerable) apparatus to the microscopic subject, Dallinger's experiment remarkably foreshadowed developments over a half-century later. At the same time, questionable antiseptic technique, iffy morphological indicators, and a design that could not differentiate Darwinism from Lamarckism prevented its widespread adoption. Dallinger did however arguably make evolution visible – his apparent sole goal. Darwin's use of breeding as natural experiment in the end was far more convincing of evolution's reality.

## Chapter 2

As biology professionalized, the methods and standards of science became more precise. Two figures especially took on this project, combining natural history with experimentation, with ideological agitating for their proposed method: Raphael Weldon and Hugo de Vries. Perhaps known more for their theories, I focused on their methods.

Weldon was a naturalist who sought to make evolution visible with statistics, a relatively new science itself. By carefully measuring animal populations, Weldon revealed subtle dimorphisms and even directional changes in sea creature populations.

His and Karl Pearson's program avoided experimentation, but his study of crabs in Plymouth Sound transitioned from a natural experiment into an actual, massive one. The aloof statistical study gave way to an interventionist experiment aimed at replicating natural changes in the crabs' environment to understand the cause and mechanisms behind the evolutionary change. In essence, they sought to avoid the excess speculation that dominated evolutionary thought, but these speculations needed to be dealt with through experimentation. Like Darwin, Weldon was not so personally interested in taking control of evolution himself, instead focused on evolution in the wild. Many biologists, particularly geneticists, rejected the "Darwinian" theory of evolution and the Pearsonian idealist research program with which he was associated, but his combination of statistics and experimentation reverberated throughout the world of experimental evolution as key to making evolution visible.

Hugo de Vries was quite different despite sharing the same interest in making evolution visible. I spent much of my discussion of de Vries revising widespread misinterpretations of his experimental work and of his mutation theory. This was important for the dissertation because de Vries' methods and ideas were among the most defining of experimental evolution's early years in the twentieth century, whether or not a scientist agreed with him (particularly Castle). Using Carolyn Merchant's formulation of control, de Vries' distinction of fluctuation and mutation was key to bringing order to the science of heredity and variation, his followers attempting to figure out how to gain power over the processes. But as I show, the distinction itself resulted from trying to experiment with and control evolution. Ironically, *Oenothera* has come to define de Vries' theory, but much of it was not experimental, and he instead constructed his theory from a wide range of botanical evidence, including horticulture, natural history, and selection experiments. Histories typically portrayed de Vries' mutation theory as a dead end and emphasize where he went wrong, but his agitation for experimentation, the promise of control, as well as his mutation theory (which was more than just saying mutations were important) were why he was so popular and impactful.<sup>768</sup> Unsurprisingly, he was invited to formally open the Station for Experimental Evolution in 1904.

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<sup>768</sup> Sharon Kingsland, "The Battling Botanist," *Isis* 82, no. 3 (1991): 479-509.

### Chapter 3

The work of Weldon and de Vries contributed to a growing sentiment among biologists that experimental evolution required significant investment in capital, land, and labor. Most calls for stations failed, but Charles Davenport succeeded in convincing the Carnegie Institution of Washington to fund his vision, a realization of Francis Bacon's dream of a New Atlantis: The Station for Experimental Evolution at Cold Spring Harbor, New York. Despite his and the Station's association with eugenics, I showed how his lengthy application materials and early lectures make no mention of the subject. Instead, Davenport elaborated upon a broad naturalistic vision of experimental evolution that searched for new principles for the purposes of understanding evolution and improving crops and livestock. The mission was to wade through the morass of contradictory evolutionary theories and mechanisms and breeding methods. He therefore considered both biologists and breeders as experimental evolution's predecessors. The point was to avoid replicating the research of the country's agricultural experiment stations, which at this time required the money of a robber baron.

Davenport's (self-admittedly) ambitious plans, the individual work of the Station's resident scientists, and the difficulties encountered in making experimental evolution work, combined to create a rather messy and confusing history. One example was George Shull's attempt to systematize the methods of Luther Burbank which ended up being a dead end. Overall, the Station's work reflected the theoretical situation of the time: the biologists published conclusions that contradicted the others. Over time though the Station settled on a Mendelian view of evolution that emphasized internal factors, genes, and chromosomes, with mutations at the forefront of change, over environmental-based theories such as the inheritance of acquired characters. Oddly, selection did not play a prominent role in the Station's work although it was not rejected or disputed as strongly as is typically portrayed at happening at that time. The explanation that Davenport offered was that the Station had focused on inheritance, perhaps too much, to the expense of variation and ecology. Thus, as messy as the Station's work was, the theory that emerged from its endeavors was far more restrictive than the epistemological pluralism that characterized Davenport's application to CIW. And at the time that I end my discussion when the Station merged with the Eugenics Record Office into the Department

of Genetics, the control of evolution remained mostly out of reach in Davenport's eyes. However, the Station and thus Carnegie did help *fund* experimental evolution's major dispute: the effects of selection on variation and heredity and its relationship to mutation.

In the last half of the dissertation, I examined in detail a decade-long debate among a set of American biologists. This debate involved William Castle, George Shull, Edward East, Herbert Spencer Jennings, and Raymond Pearl, with minor interlocuters such as the Hagedoorns, H. J. Muller, Alfred Sturtevant, and Calvin Bridges.

While the debate was theoretically over the effects of selection, it was also about *how to control evolution*. The major theories of evolution at the time suggested contradictory methods of breeding. In turn, these biologists used the breeding methods of the time to test the theories. Thus, these scientists implicitly argued that the theoretical problems would be solved through active intervention in the process (i.e., experimental evolution). A mixture of inbreeding, crossing, and selection, combined with statistical analysis, multiple generations, and environmental controls were the dominant methods of the experimental evolutionists. (A few hoped for mutation induction, but this did not come to pass in this period. See Campos and Curry for more on this project.<sup>769</sup>) Therefore, the methods of Bakewell remained the core of experimental evolution over a century later.

There were key differences between breeding and experimental evolution, however: to paraphrase Bukharin, a special mark of science is that it accumulates practice into theory. The experiments of these scientists were not at all haphazard; rather, they were guided by the major theories of evolution at the time, namely Darwinism (defined by me here as emphasizing selection as creative), Mendelism, pure line theory, and the mutation theory. As the scientists experimented, they reassessed their ideas, and even changed major positions.

I showed that Harvard geneticist William Castle served as a lightning rod around which the debate revolved due to his well-regarded zoological experimental systems of

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<sup>769</sup> Luis Campos, *Radium and the Secret of Life* (Chicago: University of Chicago Press, 2015); Helen Anne Curry, *Evolution Made to Order: Plant Breeding and Technological Innovation in Twentieth-Century America* (Chicago: University of Chicago Press, 2016).

rats, rabbits, and guinea pigs, and his increasing heretical stance against the growing Mendelian-mutationist orthodoxy. His emphasis on selection as creative, and evolution's major controllable force, was a position that these experimental evolutionists all had to contend with. While he initially theorized how mutationism and Mendelism would operate in the wild, he dropped such efforts even as he began to emphasize his version of Darwinian selection.

In parallel I discussed the botanical work of George Shull at the Station for Experimental Evolution and Edward East at the Connecticut Agricultural Experiment Station (and later Harvard's Bussey Institute, alongside Castle). Primarily (but not exclusively) focused on maize, East and Shull adopted Johannsen's pure line theory and de Vries' mutation theory as their guiding principles to investigate the interaction between inbreeding, variation and mutation, and selection. (Despite the typical portrayal of these theories, East and Shull repeatedly made clear that mutations were not defined by size, but by inheritability.) In 1908, they came to similar conclusions that inbreeding did not necessarily produce "evil effects," but instead created hereditarily stable pure lines that were immune to selection and frequently produced "evil effects" but not necessarily. In 1910, East corroborated the hypothesis of Nilsson-Ehle that continuous variation was produced by multiple factors, thus expanding the domain of Mendelism from strict alternative inheritance to more complex traits such as size. Once they incorporated genetics into their work, they argued that both selection and inbreeding reduced heterozygosity to homozygosity, but at different rates. Their continued experimentation with this evolutionary dynamic eventually produced the hybrid maize that came to dominate American agriculture – *a development of experimental evolution*.

I argue that this type of work is better thought of as experimental evolution rather than genetics. They are very similar, and soon merged (as signified by the Station for Experimental Evolution's rechristening to the Department of Genetics in 1920). But, these scientists continued a tradition that preceded genetics, were mostly interested in the *dynamics* of evolution and not just the question of variation and inheritance, and incorporated non-genetic theories – namely, mutationism and pure line theory. This is further shown by Herbert Spencer Jennings, who used organisms that at the time were not considered Mendelian organisms: the protozoa. His careful experimentation with large



numbers of organisms across several generations brought him to the same conclusions as Johannsen, but apparently independently: most visible variation was not inherited and was produced by the environment; and selection separated pure lines in a mixed population but did not *create* new lines. His work was also marked by his use of natural populations rather than domesticated plants and animals. He also worried over what I have called Jennings' Problem: because pure lines differed by *very small degrees*, he wondered how selection could *see* them when environmentally-induced variation masked them. While this problem did not dominate the debates due to its concern with evolution in nature, it popped up repeatedly as scientists thought out the implications of their work. This was exacerbated by East's crucial contribution of multiple factor theory, which brought continuous variation under Mendelian theory, and seriously undermined Castle's experiments.

Castle however was not happy with the emerging orthodoxy of pure lines and the impotence of selection, and so launched an attack that became the center of experimental evolution in the 1910s. To maintain selection's creative power, Castle argued that his opponents had no evidence that genes were stable factors immune to selection. He instead deployed his hooded rats (among other systems), which in an ongoing multiple-generation selection experiment had continued to expand or reduce the dark markings on their back, beyond the (visible) range of the parent population. From this experiment he argued that selection could change the genetic factor. Castle proposed questionable and vague mechanisms such as "potency," but eventually settled on what could be called a "sliding scale" theory of selection: because selection favored or eliminated certain variations, selection determined the course of future variation in that direction. (He usually did not articulate it this clearly, unfortunately.)

This attack and proposal received numerous counter-attacks, particularly from the up-and-coming *Drosophila* geneticist H. J. Muller, the Dutch livestock scientist Arend Hagedoorn, his former student now at the Station, E. C. MacDowell, and Maine Agricultural Experiment Station experimental evolutionist Raymond Pearl. These criticisms ranged across methods, materials, theories, and even accusations of mysticism. Beyond the specific content, this debate demonstrates how much of evolution remained up in the air theoretically and methodologically. Occasionally Castle suggested a

concession but overall hardened his views as his hooded rats experiment continued to produce favorable results. At this time Jennings began a new experiment with *Diffugia* to counter criticisms of his work and to his surprise, argued that his results were more in line with Castle than with East and Pearl. Unfortunately, though, I suggest that Jennings joined Castle in obfuscating the terms of the debate rather than engaging their opponents in good faith.

The debate waxed in a series of 1917 articles by Pearl, Jennings, and Castle, and then waned as Castle conceded in 1919. I examined Pearl's and Jennings' correspondence which highlighted the complexities of the debate, particularly over the meaning of "selection." But unfortunately, this correspondence never produced the hoped-for collaboration between the two as World War I broke out. Then a rather interesting contribution from *Drosophilist* geneticists Alfred Sturtevant and Calvin Bridges countered Jennings and Castle, who were now emphasizing the phenotypic effects of selection over the genetic mechanics that undergirded what was visible. Both Sturtevant and Bridges deployed their "breeder reactor" and chromosome mapping work; the former conducted a selection experiment in which modifying genes could be tracked, and the latter showed that the order of mutations mattered during evolution.<sup>770</sup> Lastly, another of Castle's students, Sewall Wright, who agreed more with East, suggested a hybridization experiment between the selected rats and wild rats that forced Castle to concede that selection depended on mutation, rather than selection creating the mutations themselves. In one last echo for the project of controlling evolution, Castle concluded that biologists remained "at nature's mercy." However, this one-sided lament reflected only the undermining of his own theory, rather than where evolutionary science ended in this period, with a sophisticated view of how variation, heredity, selection, mutation interacted within genetic populations. At the same time, the promise of control did not result in the hoped-for power that the Station for Experimental Evolution was tasked with investigating and developing.

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<sup>770</sup> "Breeding reactor" is Kohler's term for *Drosophila* in the Morgan laboratory in *Lords of the Fly* (Chicago: University of Chicago Press, 1994), 53.

What my dissertation has interpreted, established, and argued for is the following:

- 1) that experimentation and “experimental evolution” are at the heart of evolutionary science, and is from which much theory has developed, rather than being a later offshoot;
- 2) that Darwin should be considered a key part of the tradition of experimental evolution although he did not programmatically develop it;
- 3) that Mendel is also part of this tradition, despite being known for the static and rigid “laws of heredity,”
- 4) that both developed their methods and ideas within capitalist societies that developed systematic breeding;
- 5) that a systematic experimental evolution was conceivable in Darwin’s time, as shown by the heretofore undiscussed Reverend Dallinger, and the difficulties he faced were not unique to his time but permeate experimental evolution as a whole;
- 6) that Weldon had to face the limits of his own scientific program and had to engage in causal experimentation to understand why the changes he made visible were happening in the first place;
- 7) that de Vries’ contributions to evolution need to be further investigated on their own terms and merits rather than their purported ultimate fate, and that a full understanding of his work needs to move beyond his observations of *Oenothera*;
- 8) that biologists understood a program of experimental evolution required significant funding and lobbied state and capital for an institution to carry out this work;
- 9) that Davenport intended the Station for Experimental Evolution to take on a broad set of investigations into practice and theory during “the eclipse,” and that eugenics played little to no role in convincing the Carnegie Institution to fund such work;
- 10) that laboratory and agricultural biologists developed sophisticated methods and theories dealing with selection, mutation, inbreeding, hybridization, populations, before Fisher, Wright, and the Synthesis architects did so;
- 11) that several of them, especially East, Shull, Jennings, and Pearl contributed to the “forgotten synthesis” of Mendelian-mutationism emphasized by Arlin Stoltzfus and myself;
- 12) that while typically thought of as genetics and geneticists, it is better to interpret this period as the “time of experimental evolution” (Shull) for under debate and contention was not only the “laws of heredity,” but Mendelism as an evolutionary theory, in addition to the independently developed mutation theory, pure line theory, Lamarckism, and Darwinism (in its various guises); to interpret the work in Chapters 3-5 as genetics is thus anachronistic;
- 13) relatedly, that before *Drosophila*, key organisms in experimental evolution were poultry, *Paramecia* and *Diffflugia*, rabbits,

guinea pigs, rats, maize, potatoes, and tobacco, among others; 14) that control was a motivating factor for these scientists and the actual method by which they developed theory and interrogated their theoretical differences.

What follows are brief discussions of historiographical comments and future directions that more historical work on experimental evolution could take.

**Eugenics.** The early history of experimental evolution has obvious associations with eugenics, but the nature of that association is not so obvious. One clear connection is that Charles Davenport, who is known today *only* for eugenics, was also the captain of American experimental evolution with the power to distribute Carnegie funds. When I began this dissertation, I expected to find clearly articulated links between evolutionary experiments and eugenic policies. But as I showed in Chapter 2, Davenport's extensive application materials make no mention of eugenics. (His brief summaries of Galton, for example, include his experiments on blood transfusion and pangenesis, but nothing eugenical.) Instead, it was only after several years that Davenport began to investigate human inheritance; prior to that he was personally interested in ecology, statistics, and zoology. Therefore, I argue that the Station was latently eugenical but that the initial plans were more tied to studying evolution in nature and in the improvement of livestock and crops. Notably, though, because the dominant trend within eugenics relied on the laws of heredity, my argument that Mendel should be considered within the tradition of experimental evolution further implicates experimental evolution and eugenics. At the same time, these principles as Davenport would discuss them depended on the earliest versions of Mendelism and did not make use of the science as it had developed after 1900.<sup>771</sup>

But once eugenics became a main priority of the Station and CIW, what was the nature of the connection? Beyond using pedigrees to track information and work out Mendelian ratios, I again found no clear articulation at the Station linking the study of evolutionary dynamics and mechanisms (such as selection versus mutation) to eugenical policies, such as anti-immigration laws, mass sterilization, positive eugenics, or

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<sup>771</sup> See Davenport, *Eugenics: The Science of Human Improvement by Better Breeding* (New York: Henry Holt, 1910) as an example.

miscegenation laws. (Needless to say, the Station also never studied eugenics.) Thus, the links – in this period – are subtler. Eugenics was an easy addition for many biologists: if breeders were improving crops and livestock, then humans could also be improved.

Yet, what makes finding a direct connection between experimental evolution and eugenics is that the methodological conclusions biologists were coming to do not seem to readily apply to humans. East and Shull, for example, had articulated a breeding method that was dominated by inbreeding. Hugo de Vries ended up rejecting many eugenical conclusions because his mutation theory dismissed selection as mostly non-creative in favor of *random* mutation. Castle attacked the scientific legitimacy of eugenics, but favored eugenics for political and social reasons.<sup>772</sup> Oddly, mutation theory and pure line theory logically entailed non-eugenical views, despite producing powerful theories of evolution. Therefore, despite the broad mission of controlling evolution, how this applied to human populations was not at all clear, if not deemed impossible. This took some time for the biologists to recognize and publicize, as shown by Jennings' and Pearl's interventions in the late 1920s.<sup>773</sup> Although this still was not straightforward, as Garland Allen shows with Pearl, who attacked eugenics but transitioned to population control and continued to make racist and anti-Semitic remarks through the 1930s.<sup>774</sup>

A history such as this runs the risk of heroizing its actors. This is potentially problematic for my own dissertation given the close alignment of Davenport, East, and others with the eugenics movement. They also made their share of sexist, racist, and xenophobic remarks. So, here I acknowledge that by focusing on the science of evolution, and not the science's wider impacts, my history could appear naïve. This is heightened because I have also argued that these figures played a more important role in the history of evolution than typically ascribed to them. Mark Largent has suggested that a reason for the large blank space in the history of evolution between Weismann and Dobzhansky is due to Synthesis architects distancing themselves from the previous generations' explicit

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<sup>772</sup> Diane Paul, *Controlling Human Heredity*, 112–113.

<sup>773</sup> Diane Paul, *Controlling Human Heredity*, 70–71.

<sup>774</sup> Garland E Allen, "Old Wine in New Bottles: From Eugenics to Population Control in the Work of Raymond Pearl," in *The Expansion of American Biology*, eds. Keith R. Benson, Jane Maienschein, and Ronald Rainger (New Brunswick: Rutgers University Press, 1991): 231–61.

eugenical ties, which became especially anathema following World War II.<sup>775</sup> Thus, restoring figures such as Davenport and East into the foundations of the history of evolution could imply an endorsement of their eugenical views if not qualified and acknowledged.

**Reductionism.** I have for the most part avoided criticizing their views and their science. I am not sure of the value of criticizing 100-year-old science that has long since been modified, honed, and/or overturned, whether it is de Vries' mutation theory or the theory and practice that emerged from the debates between Castle, East, Pearl, and the others. Think, for example, of how "the gene" has undergone an incredible amount of debate, especially after the rise of molecular biology.<sup>776</sup> However, there are a few comments worth making, particularly around reductionism.

The irony of using dialectical materialism to understand the history of experimental evolution is that the science that emerged from this period was *not* dialectical in some major ways. The most obvious example is Davenport's total rejection of eugenics, the fledgling and never fully developed counter-science that emphasized social and environmental effects on human development, versus genetic determinism.<sup>777</sup> Naturalists at the time criticized the laboratory biologists for not adequately addressing the problems and questions that they faced in their own studies (notably, adaptation), that this led to theoretical missteps, and is why the laboratory biologists were non- or anti-Darwinian. Nothing I have found challenges this perception; the back-and-forth between artifice and nature of Darwin's method was not prominent among the experimental evolutionists in Chapters 4-5. I do argue that their full embrace of artificial conditions

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<sup>775</sup> Mark Largent, "The So-Called Eclipse of Darwinism," in *Descended from Darwin: Insights into the History of Evolutionary Studies, 1900-1970*, eds. Joe Cain and Michael Ruse (Philadelphia: American Philosophical Society, 2009), 3–21.

<sup>776</sup> Evelyn Fox Keller, *The Century of the Gene* (Cambridge: Harvard University Press, 2000). In my dissertation, the debates around "the gene" were over (1) whether genes could "contaminate" each other, and (2) their relative independence from the environment, (3) if the act of selection could change them directly, (4) if they could be induced to mutate. This is a far cry from whether they actually exist or how promoters, enhancers, exons and introns, etc. affect our understanding of them.

<sup>777</sup> "Apart from the fact that the truth must be faced whether pleasant or not, the contention can not be too strongly urged that improvement of conditions is only palliative, while improvement of blood is essential to permanent progress. Our only hope, indeed, for the real betterment of the human race is in better matings." From Charles Davenport, "Eugenics and Eugenics," *Popular Science Monthly* 78 (1911): 16-20.

was within the Darwinian tradition, as Bateson argued, but this should not be taken too one-sidedly; they rarely extended their findings back to evolution in the wild. But if one is interested in controlling evolution and making it useful, the question of adaptation is solved: it is whatever the breeder wants and can achieve.

However, reductionism takes on numerous guises, and when it came to evolutionary process, I suggest that they were not reductionist, but dialectical. While a cartoon version of mutationism would say that large mutations create species in a single step, the scientists I discuss rarely if ever expressed such a sentiment. Rather, they were interested in how the processes of evolution *interacted with each other*. Did selection create new variation or was its function to reduce heterozygosity? Did inbreeding always produce “evil effects” or did it have a more concrete effect on the genetics of a population? If mutations were small, could selection see them? Although these questions are somewhat naïve when compared to the questions asked by theoretical population genetics (such as variations in selection pressure) or the broader questions interrogated by the Synthesis (such as geography), it was these questions in evolutionary interactions that provided the foundation for those more sophisticated questions. I argue that while the science had its limitations, it is also an example of Levins’ and Lewontin’ description of reductionism being an extraordinarily successful aspect of science; the problem is when that reductionism is confused for how the world works as a whole, from which the experimental evolutionists did not fully escape.<sup>778</sup>

**Agriculture, Horticulture, and Breeding.** As I emphasize from the very beginning, experimental evolution and agriculture are closely linked and nearly identical,

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<sup>778</sup> Richard Levins and Richard Lewontin, *The Dialectical Biologist* (Cambridge: Harvard University Press), 1-2. The one figure in this dissertation who adamantly rejected reductionism and instead sought a more dialectical biology was Herbert Spencer Jennings. In a 1926 address as the retiring president of the Zoological Section of the AAAS, he advocated for an “Emergent Evolution” that rejected crude mechanism and determinism. He argued that biologists should adopt a “radical experimentalism” that emphasized diversity over unity. In practice, this was a retreat from eugenics and other ideas that assumed what was true of one species was true of others: that to understand humans required more than physiology, but economy, history, and politics. It was also a jab at the mechanistic conception of life propounded by Jacques Loeb. Although he did not call it dialectical, Jennings was trying to understand the contradictions of unity and diversity, mental and physical, determinism and free will, reductionism and emergence, and mechanism and vitalism. As Kingsland notes, Jennings’ advocacy for an emergent point of view foreshadowed the fight for biology’s autonomy from being reduced to physics and chemistry. See Sharon Kingsland, “A Man Out of Place: Herbert Spencer Jennings at Johns Hopkins, 1906-1938,” *American Zoologist* 27 (1987): 807-17.

as demonstrated by Bakewell and Darwin and Mendel in Moravia as has been emphasized by Theunissen, Woods, and Orel. Other figures, such as de Vries, and particularly East and Shull, developed their most important contributions within a botanical and agricultural context. A potentially important issue to study and develop is the careful distinction de Vries made between agriculture and horticulture as producing two different notions of evolution, which I mentioned in Chapter 2. But because of the laws of heredity and hybrid maize, the relationship between genetics and agriculture has been contested for decades.<sup>779</sup> The only claim I make about the impact of experimental evolution upon agriculture and horticulture is that hybrid maize *emerged from experimental evolution, not genetics*. Whether corn production required inbred hybrid maize to be more successful than with long-continued mass selection is interesting to consider but does not change the argument itself.<sup>780</sup> The consensus appears to be that genetics did not produce new breeding methods, but instead explained and rationalized existing breeding practices; but this is not really a surprise: genetics and evolution are theorizations of practice! If Theunissen is correct, for example, then Darwin's theory of evolution by natural selection is a theorization of pigeon breeding.

**Control.** A major theme that runs throughout my dissertation is that of *control*. I discussed in the introduction how control was and is a common theme among histories of biology, but was usually tucked away and not brought to the fore. Thus, I suggest that a

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<sup>779</sup> See, for example, Nils Roll-Hansen, "Theory and Practice: The Impact of Mendelism on Agriculture," *Comptes Rendus de l'Académie Des Sciences-Series III-Sciences de La Vie* 323, no. 12 (2000): 1107–16; Jonathan Harwood, "Did Mendelism Transform Plant Breeding? Genetic Theory and Breeding Practice, 1900–1945," in *New Perspectives on the History of Life Sciences and Agriculture*, eds. Denise Phillips and Sharon E. Kingsland (Cham: Springer, 2015), 345–70; Dominic Berry, "Historiography of Plant Breeding and Agriculture," in *Handbook of the Historiography of Biology*, eds. Michael Dietrich, Mark Borrello, and Oren Harman (Cham: Springer, 2018), 1–27. The volume edited by Phillips and Kingsland as a whole urges for an examination of the history of biology and agriculture *outside* of genetics, with which I heartily agree.

<sup>780</sup> One question potentially worth pursuing, and related to reductionism and dialectics, is that of the Marxist theory of metabolic rift. Developed by John Bellamy Foster, metabolic rift is the Marxist notion that capitalism has created severe rifts in the biogeochemical cycles of the environment and of the earth. Marx, for example, worried over the forced migration of English workers from the countryside to the city as disrupting the flow of nitrogen as nightsoil was robbed from the earth. Regarding my dissertation, I have come to wonder whether the systematic breeding, and the focus upon quantity of crops, dairy, and meat over qualities such as ecological sustainability, has introduced another metabolic rift. If so, then experimental evolution played a role in creating the rift, but a dialectical biology could be crucial to closing it. See John Bellamy Foster and Brett Clark, "The Robbery of Nature: Capitalism and the Metabolic Rift," *Monthly Review* 70, no. 3 (2018): 1–20; Ryan Wishart, R. Jamil Jona, and Jordan Besek, "Metabolic Rift: A Selected Bibliography," *Monthly Review*, last modified July 6, 2020, <https://monthlyreview.org/commentary/metabolic-rift/>.



comprehensive history of biological control remains to be written. This dissertation is a contribution to this theme from the perspective of late eighteenth- and early twentieth-century evolutionary biology. I argue that controlling life was relevant from Bakewell and Darwin onward and was required to make progress in understanding evolution for every step of its development. Whether or not a scientist was interested in making evolution *useful* depended on circumstances: Weldon, Jennings, and the Morgan laboratory, for example, were not, whereas Mendel, de Vries, Davenport, Castle, East, and Pearl were. This sort of division exists to this day, with Lenski's Long-Term Evolution Experiment representing the former whereas the latter is represented by the numerous projects on the industrial application of organisms such as yeast. But drawing a hard distinction has limited use: much experimental evolution both uses and interrogates bacterial and viral drug resistance. Control, both of experimental conditions and of a population's evolution, remain as central to today's experimental evolution as it did for Bakewell and Darwin.

**Dialectics.** Throughout the dissertation I have made use of dialectical materialism to understand the history of experimental evolution. This is admittedly more prominent in some sections than others, though is useful for understanding the subject throughout its history. Particularly, dialectical materialism centers labor and activity in human conduct and history, which is precisely what I argue throughout the entire dissertation: practice drove the theory. It, however, avoids one-sided pronouncements and following Bukharin, treats theory as a special form of practice. It was the active intervention upon biological populations that ultimately developed the science, this intervention being shaped by theory and in turn shaping theory. Dialectics also helped better interrogate the nefarious distinction between nature and artifice; rather than rejecting the dichotomy, I follow Darwin (and Oren Abeles' understanding of Darwin's rhetoric) in thinking of artifice as emerging from nature and thus, for example, making artificial selection a kind of natural selection. In line with what I wrote above regarding reduction, it is not so much that the experimental evolution in Chapters 4-5 were too artificial, it is that the scientists themselves did not care to link their "part" back to the dialectical whole – that awaited Dobzhansky and his cohort.

### Future Directions

Experimental evolution particularly requires further study due to its notable neglect in the history of evolution. That it has so far escaped widespread attention is rather remarkable given that the history of evolution dominates the history of biology. I addressed various reasons this is the case in the Introduction. But here I want to discuss future directions historians can take the study of this topic. I would argue that my dissertation is still *one of the first explicit and lengthy studies of experimental evolution as its sole focus*. (This is evident by the fact that Dallinger and de Varigny remain mostly unknown figures in the historical literature.) My work follows the path paved by Kohler, Kingsland, Curry, and Campos, yet requires much further elaboration.

My dissertation does not exhaust experimental evolution in the early twentieth century. While I briefly discussed a set of experiments by Davenport and Castle on the subject of Lamarckism, I ignored Lamarckism as a trend of experimental evolution. Paul Kammerer engaged in one of the most infamous (and fraudulent) experiments in evolution with midwife toads, and perhaps overshadows his contemporaries, but Sander Gliboff has revised and developed his role in the history of evolutionary science and what he represented.<sup>781</sup> One notable figure whom I had to leave out was ecologist Frederic Clements who in 1905 was among the first to use the phrase “experimental evolution.”<sup>782</sup> Clements’ use of transplantation to study evolution starkly contrasts with the breeding methods of his contemporaries. That he used it as evidence of neo-Lamarckism, and his potentially non-rigorous methodology, explains why he was not part of the mainstream discourse, but his *methods* were rather influential in the experimental study of taxonomy: another example of practice driving evolutionary science.<sup>783</sup> Another figure is William Tower, whose work Kohler shows was mired by a lack of rigor and even academic controversy. (Castle personally questioned him and Tower was evasive.) Increased focus on Clements and Tower would have likely only contributed to Kohler’s pessimistic thesis

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<sup>781</sup> Sander Gliboff, “The Case of Paul Kammerer: Evolution and Experimentation in the Early 20th Century,” *Journal of the History of Biology* 39, no. 3 (2006): 525–63.

<sup>782</sup> Frederic E. Clements and Irving S. Cutter, *Research Methods in Ecology* (Lincoln, Neb: Jacob North and Company, 1905), 12.

<sup>783</sup> Joel Hagen, “Experimentalists and Naturalists in Twentieth-Century Botany: Experimental Taxonomy, 1920-1950,” *Journal of the History of Biology* 17, no. 2 (1984), 249-270.

that experimental evolution was largely a failure, whereas I wanted to emphasize experimental evolution's key and notable contributions to the science.

**The Modern Synthesis.** Despite the extensive literature on the Modern Synthesis, its relationship with experimentation remains underdeveloped. It is widely recognized as important, but specifically *how* is usually left unsaid. For one, the debate participants such as East, Shull, Pearl, and Castle would be more widely recognized as experimentalist contributors to the Modern Synthesis if experimental evolution was more closely studied. And the neglect is somewhat surprising due to their own direct connections, including Sewall Wright being a student of William Castle's and Dobzhansky working with the Morgan laboratory. Really, the only figure I discuss who is acknowledged as having a notable impact on evolutionary thought is H. J. Muller, whose Nobel Prize winning work was conducted in the late 1920s. Sturtevant, in contrast, is noted for his taxonomic work on *Drosophila* later in his career, but his selection experiment is rarely discussed by historians, as far as I am aware.<sup>784</sup>

As for the Synthesis itself, future work on experimental evolution would likely focus on Stebbins, who conducted and relied upon an extensive set of experiments and was also sympathetic to his predecessors, recognizing the difficulties of studying heredity and variation in plants. Jean Gayon has discussed the experimental evolution of L'Héritier and Teissier who developed the population cages to understand *Drosophila*.<sup>785</sup> Provine's last book, *The "Random Genetic Drift" Fallacy*, examines a number of experiments on genetic drift by Dobzhansky's laboratory as well.<sup>786</sup> Histories of the Synthesis have predominantly focused on its social elements as well as the theoretical developments and debates, but histories of experimentation remain minimal.

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<sup>784</sup> For example, Provine notes the work in passing in *The Origins of Theoretical Population Genetics* (Chicago: The University of Chicago Press, 1971), 127.

<sup>785</sup> Jean Gayon, *Darwinism's Struggle for Survival: Heredity and the Hypothesis of Selection* (Cambridge: Cambridge University Press, 2007): 365–370; Jean Gayon and Michel Veuille, "The Genetics of Experimental Populations: L'Héritier and Teissier's Population Cages, *Thinking about Evolution: Historical, Philosophical, and Political Perspectives*, eds. by Rama S. Singh, Costas B. Krimas, Diane B. Paul, and John Beatty, vol. 2:77–102 (Cambridge: Cambridge University Press, 2001).

<sup>786</sup> William Provine, *The "Random Genetic Drift" Fallacy* (self-pub, 2014).

**Microbiology and Molecular Biology.** When starting this project, I planned to cover experimental evolution's incorporation into the emerging fields of microbiology and molecular biology that in large part characterize experimental evolution to this day. Two papers have been published on the topic: Maureen O'Malley's "The Experimental Study of Bacterial Evolution and Its Implications for the Modern Synthesis of Evolutionary Biology" and Angela Creager's "Adaptation or Selection? Old Issues and New Stakes in the Postwar Debates over Bacterial Drug Resistance."<sup>787</sup> (The latter emphasizes the lingering Lamarckism among microbiologists.) Sharon Kingsland has also devoted some attention to G. F. Gause, whose experiments with yeast and *Paramecium* led to his formulation of the competitive exclusion principle.<sup>788</sup> As I argued in the introduction, a reason I think experimental evolution has been missed by historians is that it has no real disciplinary home: if one is interested in the history of evolution, microbiology and molecular biology are not immediately obvious places to investigate.

However, there is a rich history here to explore. Scientists today such as Richard Lenski point to the 1943 publication by Max Delbruck and Salvador Luria as something of a re-founding of experimental evolution, establishing that bacteria have genetics. But other work could extend Kohler's and Curry's studies of technology and evolution by examining the invention of the chemostat by nuclear physicists Leo Szilard and Aaron Novick. (The chemostat is an instrument that houses and regulates the growth and metabolism of bacteria and is used extensively today.) Not only does this episode show the limits of disciplinary boundaries but would contribute to the literature on physicists becoming biologists after World War II, with evolution amongst them. Other projects would include studies of the former Station for Experimental Evolution under the direction of Milislav Demerec, who oriented the Cold Spring Harbor Laboratory towards experimental evolution and penicillin during World War II and hosted numerous conferences on molecular biology and bacterial genetics. More work could examine the

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<sup>787</sup> Maureen O'Malley, "The Experimental Study of Bacterial Evolution and Its Implications for the Modern Synthesis of Evolutionary Biology," *Journal of the History of Biology* 51 (2018): 319–54; Angela N. H. Creager, "Adaptation or Selection? Old Issues and New Stakes in the Postwar Debates over Bacterial Drug Resistance," *Studies in History and Philosophy of Science Part C: Studies in History and Philosophy of Biological and Biomedical Sciences* 38, no. 1 (2007): 159–90.

<sup>788</sup> Gause, G. F., "Experimental Populations of Microscopic Organisms," *Ecology* 18, no. 2 (1937): 173–79.; Sharon Kingsland, *Modeling Nature* (Chicago: University of Chicago Press, 1985).

research of Francis Ryan and Joshua Lederberg. The 1985 volume edited by Robert P. Mortlock, *Microorganisms as Model Systems for Studying Evolution*, by itself could serve as a launchpad for a history of experimental evolution involving interesting work by Patricia Clarke, Barry Hall, and Daniel Dykhuizen. What makes work such as Barry Hall's particularly interesting is that it brings evolution to Philip Pauly's remark on the organism being lost in the science: he conducted experimental evolution on molecules (beta-galactosidase). A key moment to study as well is when experimental evolution began to combine micro- and molecular biology with ecology and evolutionary biology, as done by Bruce Levin, Richard Lenski, Paul Turner, and Michael Travisano.

How to control and experiment with evolution was always a central question within the science, even if its relevance has mutated with time. Any history of evolution that centers this theme will shine new light on old subjects and reveal entirely new ones. Without focusing on experiment, Reverend Dallinger and his curious instrument remained obscured, alongside biologists usually painted as naïve geneticists but were rather critical to the development of evolutionary biology. Ideas and theories have heretofore played a prominent role in the historiography of evolution, but what is needed, in addition, is how biologists make evolution visible, controllable, and useful.

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## Appendix I: Dallinger's Machine and His Reception

### Part A. Dallinger's Machine

Once he finished his preliminary experiments, Dallinger ordered a custom apparatus from the Elliot Brothers, a thermostatic incubator outfitted with an elaborate mercury regulator.<sup>789</sup> (See Figure 10.) The primary structure consisted of three glass chambers immersed in a water-filled copper tank heated by burners beneath. A thermometer was placed in each chamber in addition to two immersed in the incubator itself. As is, this would allow for water to be heated to a certain temperature, but for Dallinger's experiment to work, the temperature needed to be kept static continuously and indefinitely for years.

The mercury regulator (on the top-left of the image) automatically governed the temperature via a thermal feedback loop. The tubes depicted within the incubator were filled with mercury and were contiguous with the tube extending vertically from the instrument. Flammable gas flowed from the top of the instrument (O) through a regulator chamber (M) and tube (N) to the burner beneath the instrument (P). In addition to heating the water within the incubator (A), the burner heated a "gridiron" of mercury-filled glass (F) (resting upon copper tubes (E)), that extended above and out of the incubator, connecting to the regular chamber (M), creating a feedback loop. Before reaching chamber (M), the mercury passed through a bulb (J) connected to a steel screw plunger (K). This chamber contained within it a smaller tube (O) housing platinum exposed to M. The gas flowed between the platinum in O and the mercury in G at level H.

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<sup>789</sup> Dallinger, 193–95. The term "cybernetic" I borrowed from Sheref Masny and Sascha Pohflepp who discuss Dallinger's instrument. Sheref Mansy and Sascha Pohflepp, "Living Machines," in *Synthetic Aesthetics: Investigating Synthetic Biology's Designs on Nature*, ed. Alexandra Daisy Ginsberg et al. (Cambridge, Mass: The MIT Press, 2014), 247–58.

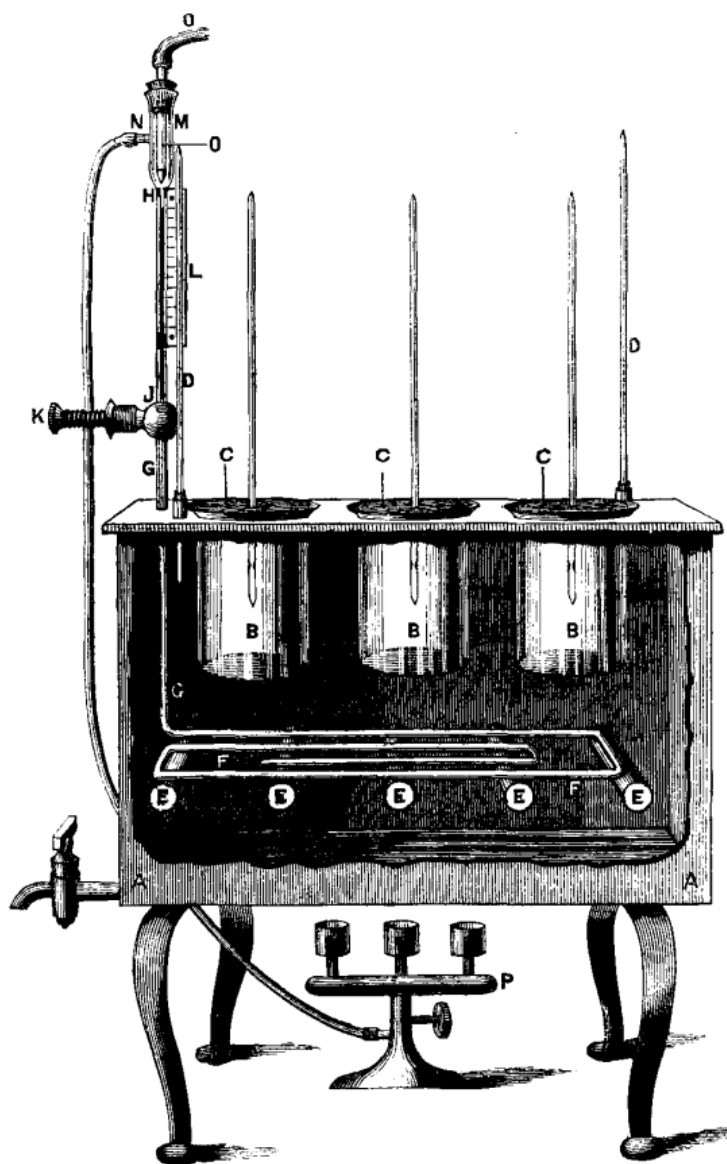


Figure 10. From Dallinger, "President's Address," *Journal of the Royal Microscopical Society* 7, no. 2 (1887), 193.

the system from turning off, keeping heat. The screw (K) is what allowed Dallinger to set the temperature of the system. According to Dallinger, the incubator could be kept within a quarter of a degree F. (In addition to this instrument, he built a hollow microscope stage that connected to the incubator, circulating heated water at the same temperature in which the organisms being examined had lived.)<sup>790</sup>

The temperature was regulated by opening and closing the gap between the platinum and the mercury. When this gap was closed, additional gas could not pass through; but, because mercury is liquid and its volume subject to changes in temperature, when the temperature decreased, the gap opened, allowing gas to flow once again. As the gas flow increased, the volume of the mercury grew with the increasing temperature, closing the gap again. Through the platinum was a tiny hole through which a small amount of gas could always flow, preventing

<sup>790</sup> William H. Dallinger, "Dr. Dallinger's Thermostatic Continuous Stage," *Journal of the Royal Microscopical Society* 7, no. 2 (1887): 317–18. Dallinger had initially constructed a similar apparatus for

## Part B. Dallinger's Reception

According to the minutes of the meeting in which he revealed his experiment, James Glashier motioned for the Royal Microscopical Society to thank and praise Dallinger for his address, to which Albert Davidson Michael seconded, who implied that such attention to detail was inhuman.<sup>791</sup> Upon his resignation as president of the Society, Francis Jeffrey Bell compared him to Darwin because his research was “a striking example of what patience, perseverance, and love a true student of nature could throw into his work.”<sup>792</sup> Some contemporary newspapers also reported his findings: *The Times* apparently had high hopes, writing “he has now extended it [the experiment] to well nigh a decade; and we may apparently look forward to future series of continuous observations being handed on from observer to observer for centuries.” The newspaper noted the power of evolutionary research on microbes, not only repeating Dallinger's claim that the work is relevant because all life is made of cells, but because of the features of the organisms: “Darwin distinctly insisted on the slowness of the process of adaptation; here we have creatures which are incessantly multiplying by dividing, the longest interval being four minutes. Dr. Dallinger must therefore have observed something like half a million generations of the organisms under consideration. Here are the “countless generations” required.”<sup>793</sup> They concluded that from his research, despite his protests of limited application, “an endless vista of possible adaptations is opened up.” *The Northern Echo* praised Dallinger's meticulous skill and scientific attitude, his work “one more striking confirmation of his [Darwin's] doctrine of the origin of species.”<sup>794</sup>

Following this immediate praise, mentions of Dallinger's experiment are fragmentary and rare. Ironically, when discussed, his work was interpreted as support not for Darwinism, but for the inheritance of acquired characters! Manly Miles, for example,

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the purpose of studying a “septic organism” at its normal temperature, 90-95° F.

<sup>791</sup> *Journal of the Royal Microscopical Society for the Year 1887*, vol. 1 (London: Williams and Norgate, 1887), 354. James Glashier was an astronomer, meteorologist, balloonist, and photographer who had previously served as the Society's president. Albert Davidson Michael was an amateur naturalist and founding figure of acarology (mites and ticks) who served as the society's president following Dallinger. (Other previous presidents included Richard Owen, William B. Carpenter, and Edwin Lankester.)

<sup>792</sup> *Journal of the Royal Microscopical Society for the Year 1887* (London: Williams and Norgate, 1888), 328.

<sup>793</sup> “The Royal Microscopical Society,” *The Times*, February 14, 1887.

<sup>794</sup> “The Infinitely Great and the Infinitely Small,” *The Northern Echo*, February 15, 1887. Both articles are striking for their detailed description of Dallinger's experiment.

claimed the experiment showed

that the modified or acquired habits or organisms are beyond question transmitted to their offspring. ... At times a slight increase of temperature was not tolerated until the changed habits of their protoplasm provided for the complete adjustment of their vital activities to the new environment. ... It is evident that the germ plasma was affected by the changes in the environment, either directly, or with greater probability through the modified metabolism of the body plasma.<sup>795</sup>

C. C. Nutting also claimed that if August Weismann's distinctions between somatogenic and blastogenic characters were true, in which the former included "changes ... directly due to nutrition and any of the other external influences which act upon the body," then "the increased toleration of a high temperature shown by the bacteria in Dr. Dallinger's experiments, would be an acquired character, and that this character was transmitted was experimentally proven."<sup>796</sup> Frederick Headley, in *Problems of Evolution*, also cited Dallinger's experiment as Lamarckian, although it "admits of a non-Lamarckian interpretation. Natural selection was no doubt at work."<sup>797</sup> However, because of fission, "the last generation belonged also to the first: they were fragments of the individuals that existed at the outset." Therefore, "we have here merely the gradual acclimatisation of one individual."<sup>798</sup> A. S. Packard in a letter to the editor of *Science*, advocating for the Carnegie Institution of Washington to fund "pure, unapplied biology," such as the "researches ... in temperature experiments in the line of the splendid researches of Dallinger, Weismann, Standfuss ..., who have wellnigh demonstrated the actual process of species, variety, and racemaking."<sup>799</sup> That Packard acknowledged Dallinger makes Davenport's lack of citation all the more intriguing.

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<sup>795</sup> Manly Miles, "Heredity of Acquired Characters," *The American Naturalist* 26, no. 311 (1892): 897–99.

<sup>796</sup> C. C. Nutting, "What Is an 'Acquired Character?'," *The American Naturalist* 26, no. 312 (1892): 1010. In an obituary, Arthur Shipley wrote that Dallinger had opposed August Weismann's anti-Lamarckism, but I have not located any documents showing this.

<sup>797</sup> Frederick Webb Headley, *Problems of Evolution* (London: Duckworth, 1900), 43.

<sup>798</sup> Headley, 44.

<sup>799</sup> Bashford Dean et al., "The Carnegie Institution," *Science* 16, no. 408 (1902): 647.